"Paradox Lost": Skeletal Ontogeny of *Indostomus paradoxus* and Its Significance for the Phylogenetic Relationships of Indostomidae (Teleostei, Gasterosteiformes)

RALF BRITZ[1] AND G. DAVID JOHNSON[2]

How wilt thou reason with them, how refute
Their idolisms, traditions, paradoxes?

John Milton, *Paradise Regained*, 1671

On the Use of Ichthyology
Utility will always be found to depend more on the degree of attention to any subject connected with science, than on the nature of the subject itself; yet it is a common remark that this, or that, is important or frivilous, according as we happen to be acquainted with it. When we find any branch of science regarded as useless, we may be assured that, contrary to ordinary expectation, it will prove the most productive field we can enter. Science, indeed, can only be useful where it has been cultivated, and its principles worked out; practical results will then follow in proportion to the pains taken to develop them.

John McClelland (1839: 457)

[1] Assistant Professor, Lehrstuhl für Spezielle Zoologie, Universität Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany; Research Associate, Division of Vertebrate Zoology (Ichthyology), American Museum of Natural History. Present address: Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington D.C. 20560, e-mail: Britz.Ralf@nmnh.si.edu
[2] Curator, Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington D.C. 20560, e-mail: Johnson.Dave@nmnh.si.edu

ABSTRACT

On the basis of an ontogenetic series of *Indostomus paradoxus*, we test characters that have been proposed for the phylogenetic placement of this enigmatic taxon. Contrary to previous authors, we found that the body armor of *Indostomus* differs from that of syngnathoids greatly and it closely resembles that of gasterosteoids in many unique details. The body plates originate from two different sources, that is, the endoskeleton (proximal-middle radials of dorsal and anal fin, neural and hemal spines, pelvic cartilages) and the exoskeleton (postcleithra, lateral body plates, sternal plate). The median bone in the ethmoid region develops from two centers and most likely represents the nasal bones that fuse during ontogeny with each other and with the vomer. Identity of the opercular bones is clarified, and it is demonstrated that *Indostomus* has an interopercle. The single pterygoid bone is the ectopterygoid. A parietal is lacking. There is only one cartilaginously preformed hypural element in the caudal fin. There is no parhypural, but a similar structure, termed the pseudoparhypural by us, develops as membranous outgrowths of the single hypural and the ural centrum. The pectoral radial plate fuses to the scapulocoracoid cartilage, and the pectoral radials ossify within that fused plate without prior fragmentation of the plate into individual radials, being specializations of the pectoral girdle that we think to be shared with all gasterosteoids. *Indostomus* shares with other gasterosteiforms the modification of the tripartite occipital condyle into an articulation of the basioccipital and the first centrum through loss of the articulation between exoccipitals and the first centrum in all developmental stages. *Indostomus* lacks distal radials in all pterygiophores supporting fin spines at all developmental stages, a character shared with other gasterosteiforms, mastacembelids, and probably other smegmamorphs. We conclude that *Indostomus* is a gasterosteoid gasterosteiform.

INTRODUCTION

In 1926, a party of the Zoological Survey of India collected numerous specimens of a small pipefishlike fish in Lake Indawgyi (Upper Myanmar), which was later described as *Indostomus paradoxus* Prashad and Mukerji, 1929 (fig. 1). Because of its unique appearance, the authors placed it in the new family Indostomidae. Prashad and Mukerji (1929: 219) considered *Indostomus* to be "closely allied to the family Solenostomidae and to a certain extent to the Syngnathidae."

Bolin (1936: 420) concluded that "Prashad and Mukerji erred" and that Indostomidae showed closer affinities to less specialized gasterosteiforms such as Aulorhynchidae and Aulostomidae. This view was accepted by subsequent researchers (see Berg, 1958; Bertin and Arambourg, 1958; Greenwood et al., 1966) until Banister (1970), studying the osteology of *Indostomus* in more detail, proposed a closer relationship of this taxon with some Paracanthopterygii. Fraser (1972) pointed out that most of Banister's arguments for excluding *Indostomus* from the Gasterosteiformes are negative (loss) characters and he therefore left the In-

dostomidae incertae sedis. The idea of a closer relationship between *Indostomus* and the gasterosteiforms was revived by Pietsch (1978) and supported subsequently by Johnson and Patterson (1993) with additional characters.

The latter authors found that among gasterosteiform subgroups *Indostomus* shares apomorphic features with the Syngnatha sensu Pietsch (1978) and additional ones uniquely with the Pegasidae. Bowne (1994: 56) thought that "*Indostomus* might belong with either the syngnathid-solenostomid or aulostomid-fistulariid lineages." In contrast, Orr (1995) again saw no evidence to retain *Indostomus* in the Gasterosteiformes.

The main reason for these widely differing views on the placement of *Indostomus* is its highly derived adult morphology. This makes it difficult, if not impossible, to decide between the different hypotheses without knowledge of ontogeny of the bones in question. A recent successful rearing of *Indostomus paradoxus* (fig. 1A; Britz, 2000) has yielded an ontogenetic series that now enables us to check Johnson and Patterson's (1993) homology propositions and interpret the findings in a phylogenetic framework.
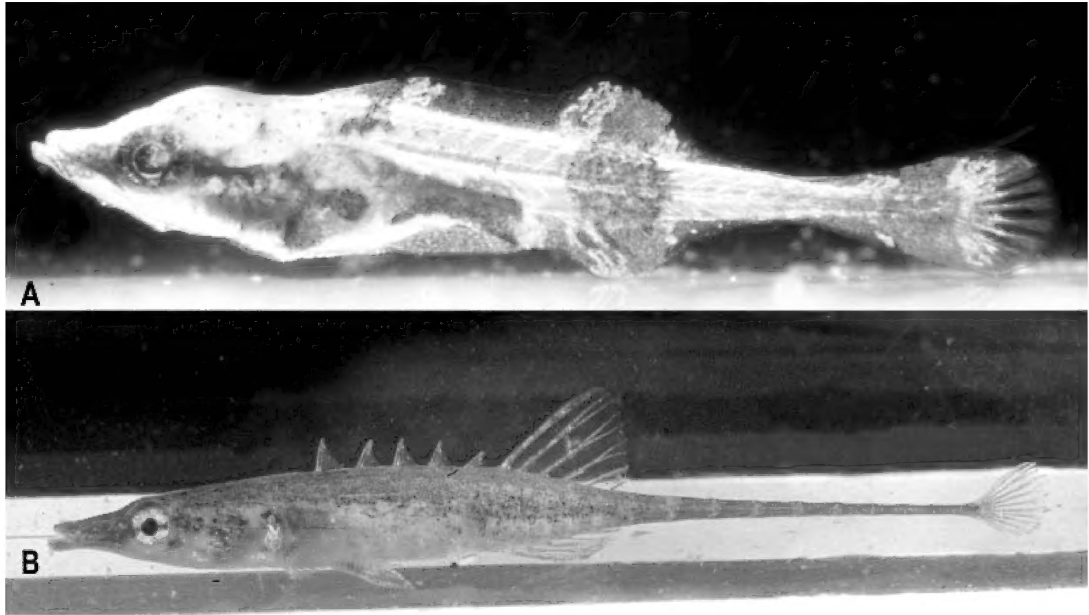
Fig. 1. *Indostomus paradoxus*. **A.** Larva, ca. 4.5 mm, with typical larval pigment pattern. **B.** Adult, ca. 28 mm.

MATERIALS AND METHODS

Indostomus paradoxus were maintained and spawned as detailed by Britz (2000). From hatching on, larvae were preserved at regular intervals in 4% buffered formalin for several days, run through an alcohol series (30%, 50%, 70%), and stored in 70% ethanol. Sixteen developmental stages of *I. paradoxus* ranging from 3.0-mm total length (TL) to 11.2-mm standard length (SL) were selected for clearing and double-staining (C&S) and prepared according to the protocol of Taylor and van Dyke (1985) or Springer and Johnson (2000). The ontogenetic material was supplemented by a 16.6-mm juvenile (NRM 41012) and several full-grown C&S specimens (see list below) of all three *Indostomus* species (Britz and Kottelat, 1999).

For SEM, skeletal parts of C&S specimens of *I. paradoxus*, USNM 366875 (27, 28, 32 mm), and *I. spinosus*, USNM 366876 (28 mm), were removed. The bone was cleaned from the adhering tissue by a short treatment with 1% $NaHCl_3$ for about 10 minutes under stereomicroscopical control. Bones were either dehydrated in a graded series of ethanol and critical-point dried with liquid CO_2 in a Polaron E 3000 series II or they were just dried in air. After drying, bones were mounted on aluminum stubs. The mounts were then coated with 20-nm gold-palladium in a Balzers SCD 030. They were observed and photographed using a Cambridge Stereoscan 259 MK2.

Color photos of C&S specimens were made with a Zeiss Tessovar or with a Zeiss Axioplan compound microscope.

Nomenclature for the elements of the chondrocranium follows Gaupp (1906) and de Beer (1937). All lengths are SL unless otherwise stated. In all illustrations, anterior faces left unless indicated otherwise. Institutional abbreviations follow Leviton et al. (1985).

Cleared and double-stained specimens of the following species were used in this study. Anabantidae: *Ctenopoma* cf. *pellegrini*, USNM 367057 (1, 8 mm); Aulorhynchidae: *Aulichthys japonicus*, UW 22061 (2, 98 mm, 120 mm); *Aulorhynchus flavidus*, BMNH 1979.7.20.7 (1, 92 mm); *Aulorhynchus flavidus*, USNM 344688 (2, ca. 138 mm, 150 mm); *A. flavidus*, USNM 366870 (33, 4.2 mm NL [notochord length]–38.5 mm); *A. flavidus*, UW 22058 (6, 67–87 mm); Aulo-

stomidae: *Aulostomus* sp., USNM 364535 (1, 83 mm); *A. maculatus*, USNM 344482 (1, 132 mm); Centriscidae: *Centriscus* sp., USNM 329716 (4, 33–107 mm); Elassomatidae: *Elassoma zonatum*, AMNH 79013 (7, 8–13.5 mm); Fistulariidae: *Fistularia* sp., USNM 366897 (2, 126 mm, 195 mm); Gasterosteidae: *Apeltes quadracus*, USNM 200737 (5, 29–30 mm); *Culaea inconstans*, USNM 069287 (1, 46.5 mm); *Culaea inconstans*, USNM 196818 (5, 38.5–40.5 mm); *Gasterosteus aculeatus*, HSU 0259 (18.6 mm NL–16.5 mm); *G. aculeatus*, USNM 366872 (50, 5.6 mm NL–40 mm); *G. aculeatus*, ZMB 24126 (1, 42 mm); *Pungitius pungitius*, USNM 077842 (3, 34.5–55 mm); *Spinachia spinachia*, USNM 344839 (1, 90 mm); *S. spinachia*, USNM 344840 (1, 119 mm); *S. spinachia*, USNM 366871 (4, 19–33 mm, 121 mm); Hypoptychidae: *Hypoptychus dybowskii*, BMNH 1979.9.4.14 (1, 64 mm); *H. dybowskii*, UW 029655 (3, 60–69 mm); Indostomidae: *Indostomus crocodilus*, USNM 366874 (10, 20–25.5 mm); *I. paradoxus*, NRM 41012 (1, 16.6 mm); *I. paradoxus* USNM 348212 (6, 24–27 mm); *I. paradoxus*, USNM 366869 (16, 3.0 mm TL–11.2 mm); *I. paradoxus*, USNM 366875 (17, 25–33 mm); *I. spinosus*, USNM 366876 (5, 24–29 mm); Macroramphosidae: *Macroramphosus scolopax*, USNM 364362 (2, 70 mm, 76 mm); Mastacembelidae: *Macrognathus pancalus*, USNM 367058 (1, 16.7 mm); Pegasidae: *Eurypegasus papilio*, USNM 340849 (1, 31 mm); *Pegasus laternarius*, ZRC 40314 (1, 50 mm); *Pegasus volitans*, USNM 147848 (1, 51 mm); *Pegasus volitans*, ZRC 2332 (1, 63 mm); Solēnostomidae: *Solenostomus* sp., USNM 320116 (1, 22 mm); *S. paradoxus*, AMS I.18314002 (1, 55 mm); Syngnathidae: *Coelonotus platyrhynchus*, USNM 091835 (3, 98–100 mm); *Urocampus carinirostris*, USNM 215310 (2, 55 mm, 64 mm); *Syngnathus typhle*, USNM 366873 (1, 121 mm).

Abbreviations

ACh	anterior ceratohyal
An	angular
Ana	anguloarticular
APl	anal plate
Asph	autosphenotic
Bb	basibranchial
BbC	basibranchial cartilage
Bh	basihyal
Boc	basioccipital
BR	branchiostegal ray
Cb	ceratobranchial
CC	copula communis
Cl	cleithrum
Cm	coronomeckelian
Co	coracoid
De	dentary
DHh	dorsal hypohyal
DR	distal radial of pterygiophore
Eb	epibranchial
EbC	epibranchial cartilage
Ecpt	ectopterygoid
Epoc	epioccipital
EpC	epiphyseal cartilage
EthPl	ethmoid plate
Exoc	exoccipital
FH	fenestra hypophyseos
Fr	frontal
H	hypural
Hb	hypobranchial
HbC	hypobranchial cartilage
HhC	hypohyal cartilage
HS	hemal spine
HsyC	hyosymplectic cartilage
Hy	hyomandibular
Ih	interhyal
IhC	interhyal cartilage
ImB	intermuscular bones
Iop	interopercle
LE	lateral ethmoid
LO	lamina orbitonasalis
LPl	lateral plates of body armor
MC	Meckel's cartilage
Mpt	metapterygoid
Na	nasal
NS	neural spine
OF	olfactory foramen
Op	opercle
PA	pars autopalatina of palatoquadrate
Pb	pharyngobranchial
PCh	posterior ceratohyal
Pcl	postcleithrum
PcoPr	postcoracoid process
PF	pelvic fin
P-MR	proximal-middle radial of pterygiophore
PMpt	pars metapterygoidea of palatoquadrate
Pop	preopercle
Pph	pseudoparhypural
PPl	pelvic plate
Pq	palatoquadrate
PQ	pars quadrata of palatoquadrate
PR	pectoral radial
Pro	prootic

PRPl	pectoral radial plate
Psph	parasphenoid
Pt	posttemporal
Pto	pterotic
PU	preural centrum
PvPr	posteroventral process
Q	quadrate
R	fin soft ray
Ra	retroarticular
S	fin spine
Sc	scapula
SccoC	scapulocoracoid cartilage
Scl	supracleithrum
Soc	supraoccipital
Sop	subopercle
SPl	sternal plate
Sy	symplectic
Tr	trabecula
TrC	trabecula communis
TPr	transverse process
TS	tectum synoticum
U	ural centrum
UP4	fourth upper pharyngeal toothplate
V1	first vertebra
VHh	ventral hypohyal
Vo	vomer

RESULTS

Ontogeny of Neurocranium

We restrict our description of the development of the neurocranium to those stages that yield evidence to evaluate the controversial homology of several bones.

The first specimen we figure is 4.8 mm (fig. 2A; pl. 1A). At this stage there is a broad, almost rectangular ethmoid plate with a prominent posteriorly curved process projecting laterally from each of its anterior corners. The ethmoid plate ascends posteriorly, giving rise to the rounded, laterally projecting laminae orbitonasales, each enclosing a foramen for the olfactory nerve. Paired, elongate, dermal ossifications, putatively the nasals, overlie almost the complete length of the ethmoid plate. They do not bear a lateral line canal at this or any subsequent stage. Their posterior pointed tips extend slightly past the anteromedial pointed tips of the frontals. Although present, the vomer is not visible in dorsal view. The frontals cover the lateral sides of the orbital skull roof and span from the anterior corner of the auditory capsule to the upper end of the laminae orbitonasales. They have a roughly triangular shape

and exhibit some sculpturing on their dorsal surface. Their medial arms do not contact each other but approach the midline where they partly cover the triangular autogenous remnant of the epiphyseal cartilage. Neither an epiphyseal bridge nor a taenia marginalis anterior is present.

Ventrally, the orbital region of the skull consists of the fused cartilaginous trabeculae underlain by the parasphenoid. Posteriorly, the trabecula communis splits into the individual trabeculae, which form the anterior border of the fenestra hypophyseos and connect posteriorly to the basal plate of the skull. The parasphenoid covers the fenestra hypophyseos ventrally. It bifurcates posteriorly, and the two parasphenoid arms run parallel to the anteriormost tip of the chorda, which projects into the fenestra hypophyseos. On the basal plate lateral to its confluence with the trabeculae a large foramen is developed. The prootic is ossified around this foramen and covers the cartilage as a circular perichondral ossification. The autosphenotic is ossified at the postorbital process of the auditory capsule. The skull roof of the otic region is still open and the auditory capsules of the left and right side do not meet in the midline. Their posterolateral parts are ossified as the pterotics. We cannot say from our limited sample of ontogenetic stages if the two components of the pterotic (auto- and dermopterotic) are present. The pterotics each bear two blunt spines at their lateral edges, with the posterior one being more prominent. In the occipital region, the exoccipitals are ossified to the left and right of the foramen magnum. Their posterior parts project as pointed processes of membrane bone. The basioccipital is ossified around the cranial portion of the chorda and from there spreads into the cartilage of the basal plate as two semicircular perichondral ossifications.

The second specimen we illustrate here is 6.4 mm (fig. 2B). It differs fundamentally from the preceding stage as follows. The nasals are fused to each other and to the vomer anteriorly (compare also pl. 1A–C). Their posterior parts remain separate from each other and their posterior tips just contact the frontals. The vomer now wraps around the anterior end of the ethmoid plate from its
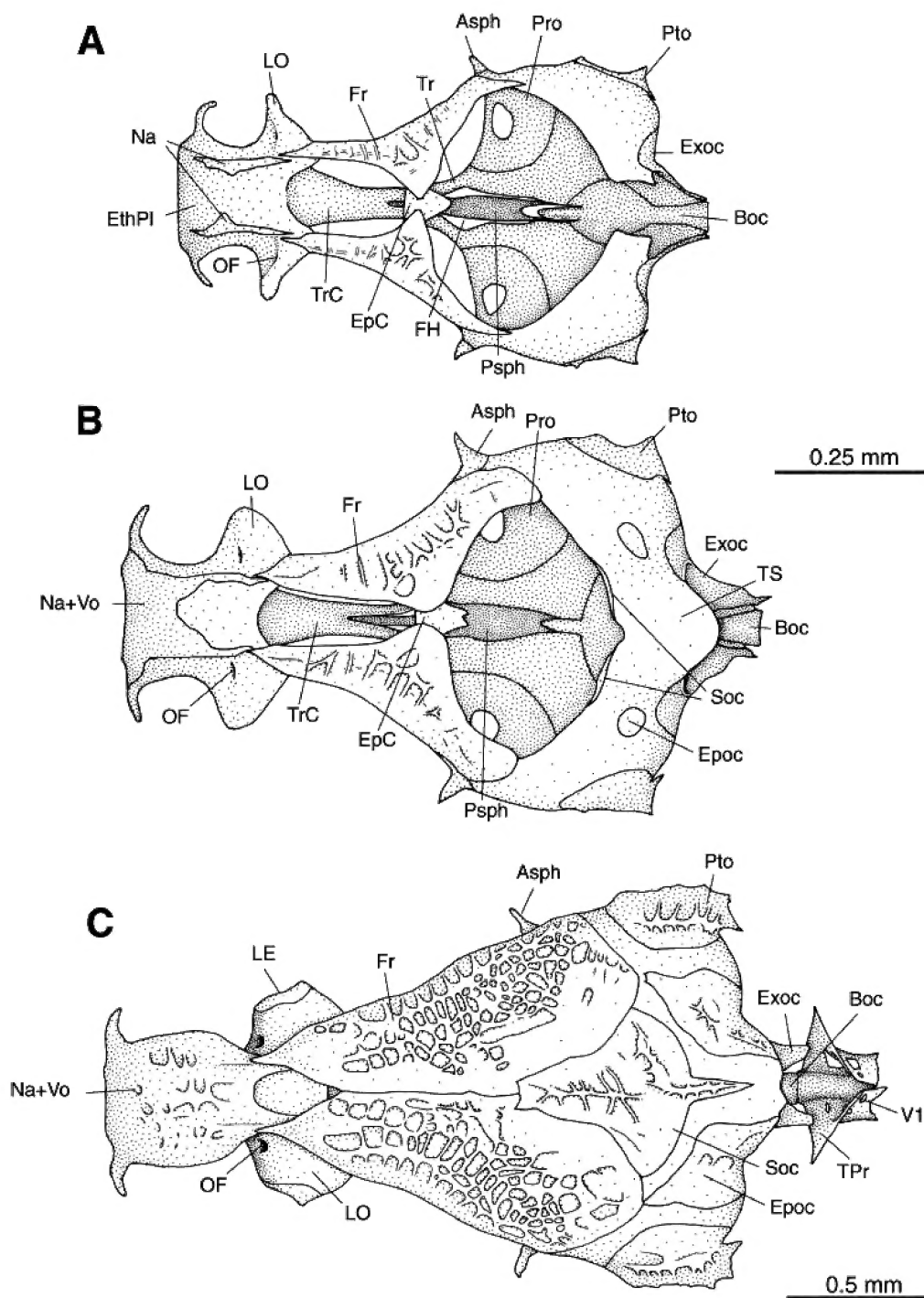
Fig. 2. *Indostomus paradoxus* (USNM 366869). Developmental stages of neurocranium in dorsal view. Bone gray, cartilage white. **A.** 4.8 mm. **B.** 6.4 mm. **C.** 11.2 mm.

ventral surface to its dorsal face where it is now fused to the nasals. The lateral processes at the anterior corners of the ethmoid plate remain cartilaginous. The more extensively sculptured frontals have expanded medially but still do not contact each other in the dorsal midline. All endoskeletal ossifications of the skull have spread into larger areas of the cartilage. The auditory capsules are connected to each other dorsally in the occipital region, thus forming a tectum synoticum. In the midline of the anterior edge of this tectum the supraoccipital has ossified. In our specimen two separate areas to the left and right of the midline are stained with Alzarin. However, other specimens of similar size showed only one center of ossification. We cannot exclude the possibility that the area between these separate ossifications in our 6.4-mm specimen contains unstained bone. About halfway between the pterotics and the dorsal midline, the epioccipitals appear as circular perichondral ossifications. On the exoccipitals, the posterior processes of membrane bone are more prominent.

The third stage we illustrate is 11.2 mm (fig. 2C). The complex of the fused nasals and vomer now covers the whole ethmoid plate, including the lateral processes. The dorsal surface of the complex shows the first traces of the sculpturing typical of all superficial bones. The complex still has the two posterior processes that stem from the nasals, and their posterior tips are covered by the anterior tips of the frontals. The lateral edge of the lamina orbitonasalis is ossified as the lateral ethmoid. The frontals contact each other in the midline along most of their length. In their posterior third they separate and the supraoccipital is wedged in between the frontals. The pterotics, epioccipitals, and supraoccipital are much larger relatively, and only small strips of cartilage are still present between them. All dorsal skull bones possess the typical surface ornamentation. The posterior processes of the exoccipitals are more prominent now and have started to form an articulation with the anteriorly expanded transverse processes of the first centrum.

ONTOGENY OF OCCIPITAL ARTICULATION WITH FIRST VERTEBRA

In our 4.8-mm specimen, the articulation of the occipital region with the first vertebra

is only through the basioccipital (fig. 2A). The caudal ends of the exoccipitals project as acute processes of membrane bone without reaching the first vertebra (see also 5.3-mm specimen, pl. 1D). These processes project farther in the 6.4-mm specimen (fig. 2B) but still fail to contact the first vertebra. In the 11.2-mm specimen they have lengthened farther and widened so that their distal tips are spatulate, and they extend a little beyond the anterior edge of the transverse process of the first vertebra, which has flattened and widened its anterior area (fig. 2C). In the adult, the posterior exoccipital processes are conspicuously broad and flat (fig. 3A–C) and articulate with the dorsal side of the transverse processes of the first vertebra (fig. 3D–F). To receive the exoccipital processes, the latter have two roundish wide articulatory sockets on their broad bases (fig. 3E, F). Processes and sockets are tightly connected to each other.

ONTOGENY OF HYOPALATINE ARCH

The bones of the hyopalatine arch in adult *Indostomus paradoxus* were described by Banister (1970). He found that, unlike the typical percomorph condition, there is only one large elongate bone anterior to the quadrate. Banister (1970) was unable to decide whether this bone represents the endopterygoid, the ectopterygoid, the palatine, or a product of fusion of some or all of these bones. The opercular series is also unusual in that there is a tiny splintlike subopercle situated at the posterodorsal edge of the large opercle. The bone Banister (1970) identified as the interopercle also is unusually high and wide, fits tightly into the space between the lower jaw and the opercle, and forms the posteroventral border of the orbit. This led Johnson and Patterson (1993) to identify Banister's (1970) interopercle as the preopercle and his preopercle (a rectangular bone) as an infraorbital.

The smallest specimen we studied is 3 mm (fig. 4A). Of the palatoquadrate, only the pars quadrata and metapterygoidea are present. The pars autopalatina is not developed. The lowermost tip of the pars quadrata articulates with Meckel's cartilage. The two dermal components of the lower jaw, dentary

and angular, are present. The dentary bears no teeth. The hyosymplectic cartilage has a long dorsal head for articulation with the auditory capsule of the neurocranium. It is pierced by the foramen of the hyomandibular trunk of the facial nerve. Its posterior part articulates with the opercle. The symplectic process extends alongside the quadratometapterygoid cartilage. The opercle is ossified and trifurcates posteriorly into pointed spinelike processes, with the upper one pointing dorsoposteriorly, the middle one horizontally, and the lower one ventrally. Bony ridges extend from the proximal articulation of the opercle to the pointed processes. A thin splint of bone, the subopercle, reaches from the incisure between the lower and the middle process of the opercle almost to its upper process. It is covered laterally by the tip of the middle spine.

In the 3.3-mm specimen (fig. 4B), the pars autopalatina is present as an autogenous rod of cartilage well removed from the pars quadrata. The pars metapterygoidea has a prominent dorsal process. The angular of the lower jaw now extends farther anteriorly along the ventral edge of Meckel's cartilage. The dentary bifurcates posteriorly. Its lower limb runs ventral to Meckel's cartilage and extends ventral to the anterior tip of the angular. The opercle is larger but similar in shape. The subopercle has elongated without increasing its relative width and reaches ventrally beyond the tip of the lower process of the opercle.

In the 4.3-mm larva, the pars autopalatina is fused to the pars quadrata (fig. 4C). Only a small foramen is present in the upper third of the contact zone. Ventral to the pars autopalatina is a small splint of bone, the developing ectopterygoid. The quadrate has os-

sified at the jaw joint and covers the lower third of the quadratometapterygoid cartilage. In the hyosymplectic cartilage there are two ossifications, the hyomandibular at the level of the facial foramen, and the symplectic at about the middle of the symplectic process. The tip of the symplectic process remains cartilaginous. The opercle is larger with some evidence of ornamentation and has an additional short pointed process on its anteroventral margin just anterior to the lower process described above. The interopercle is ossified as a thin horizontal splint of bone lying between the opercle and the lower jaw (pl. 1E, F). Its anterior tip lies in the mandibulohyoid ligament, which originates from the ceratohyal and inserts at the posteroventral tip of Meckel's cartilage where the retroarticular has formed (see pl. 1H). The angular is now longer and covers most of the lateral side of Meckel's cartilage. An articular ossification is not evident at this stage. The dentary bears several posteriorly directed pointed teeth at its anterior end, and its two posterior process are notably longer.

In the 5.5-mm specimen the primary differences from the preceding stage involve the relative growth of some of the bones (fig. 5A). The ectopterygoid remains a narrow splint but now extends forward beyond the anterior tip of the autopalatine cartilage. The quadrate extends slightly into the autopalatine cartilage and has a tiny foramen, probably a remnant of the relatively larger foramen of the last stage. The metapterygoid has ossified around the posterior tip of the pars metapterygoidea. The hyomandibular bears a flange of bone posterior to the facial foramen. The anastomosing ornamentation of the opercle is more extensive. The subopercle is little changed. The interopercle is deeper,

→

Fig. 3. *Indostomus*. SEMs of occipito-vertebral articulation and anterior vertebrae. **A.** *I. spinosus*, 28 mm (USNM 366876), neurocranium, ventral view, anterior to right. **B.** Same specimen, close-up of ventral occipital region, anterior to right. **C.** Same specimen, close-up of ventral occipital region, posterior view. **D.** *I. paradoxus*, 27 mm (USNM 366875), vertebrae one to three, dorsal view. **E.** *I. paradoxus*, 28 mm (USNM 366875), shoulder girdle with first vertebra attached, frontal view; note that transverse process of vertebra is tightly bound to medial face of cleithrum through a short ligament. **F.** Same specimen, articular facets of transverse process and centrum, frontodorsal view. **G.** Same specimen, close-up of left articular facet to show spongy appearance of bone. **H.** *I. paradoxus*, 28 mm (USNM 366875), vertebrae two and three, lateral view.
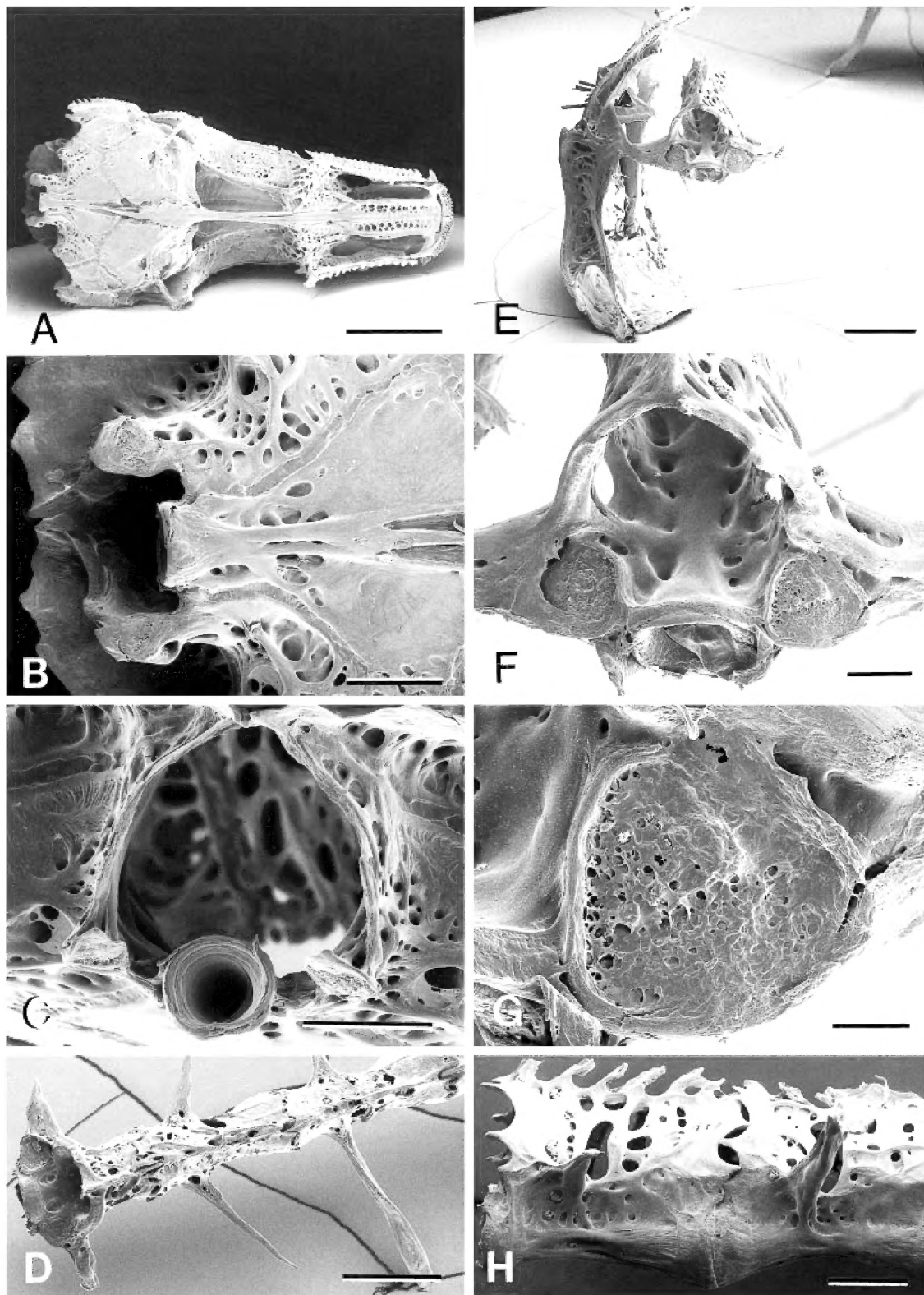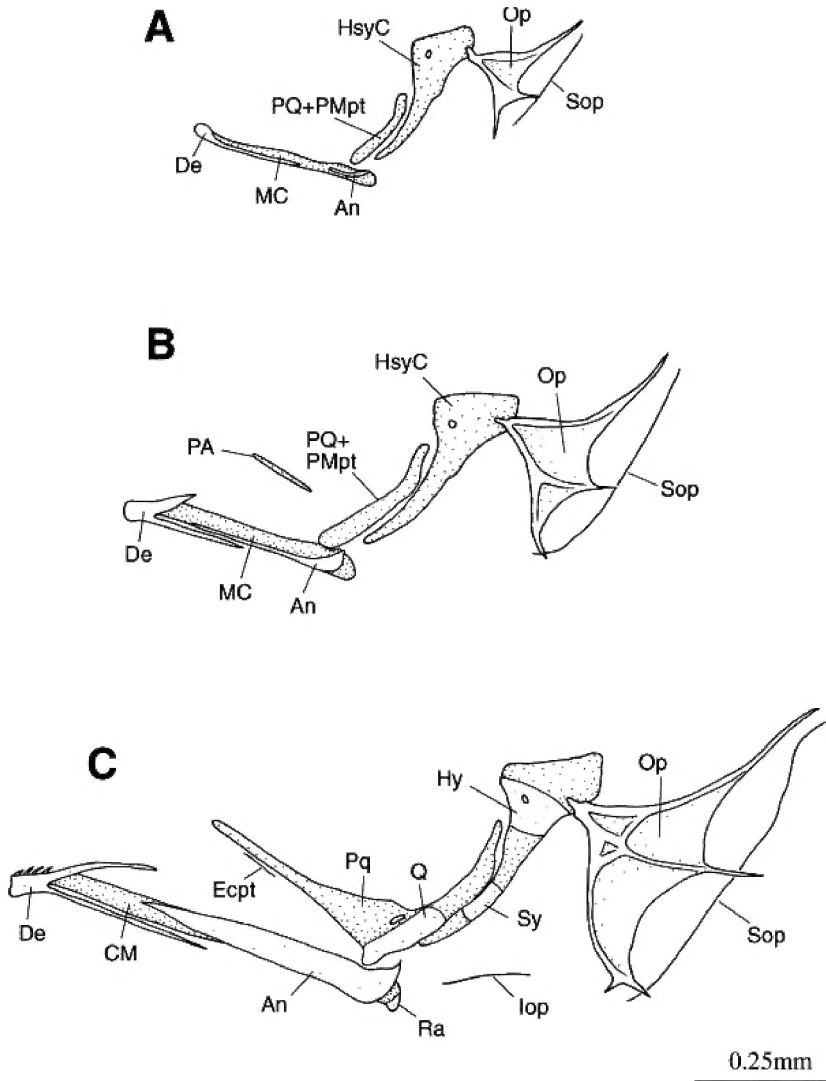
Fig. 4. *Indostomus paradoxus* (USNM 366869). Ontogeny of hyopalatine arch and lower jaw, lateral view. **A.** 3.0 mm. **B.** 3.3 mm. **C.** 4.3 mm.

longer, and slightly crescentic in shape. The dentary bears more teeth, and the deep cleft between its two posterior processes is closed by bone over most of its length. The corono-meckelian bone is ossified as a small bony rod in an unusual spot. It is shifted dorsally from the normal position at Meckel's cartilage into the tendon of the A3 section of the adductor mandibulae, so that it lies at the level of the palatoquadrate. Ossification of Meckel's cartilage around the jaw joint implies that the endoskeletal articular has ossi-

fied thus with the dermal angular forming the anguloarticular bone of the lower jaw.

In the 8.7-mm specimen (fig. 5B), the ectopterygoid is longer and deeper, possesses a prominent pointed anterior process, and covers the pars autopalatina medially along almost its entire length. Only its anteriormost dorsal tip projects from the ectopterygoid. The ossification of the quadrate extends into the proximal area of the pars autopalatina. The metapterygoid bears a low ridge of membrane bone along its anterior edge. The opercle is relative-
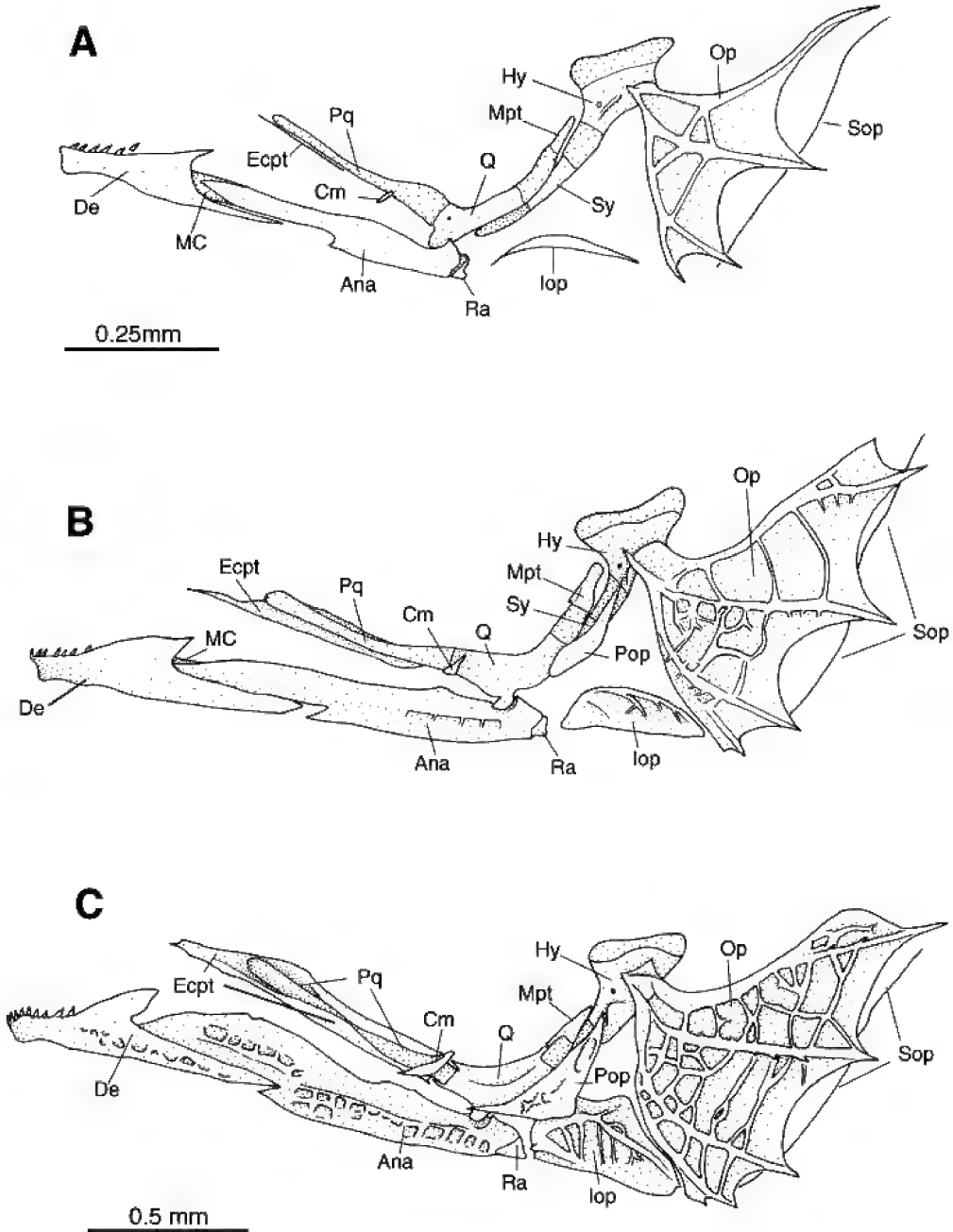
Fig. 5. *Indostomus paradoxus* (USNM 366869). Ontogeny of hyopalatine arch and lower jaw, continued, lateral view. **A.** 5.5 mm. **B.** 8.7 mm. **C.** 11.2 mm.

ly larger and more extensively ornamented. The subopercle is little changed. The interopercle is longer, deeper, roughly rectangular, and exhibits some ornamentation. Along the ventral part of the hyosymplectic, the preopercle has ossified (see also pl. 1G, H). It is an elongate bone with a pointed upper tip that is attached to the bony flange on the hyomandibular. The posterior third of the anguloarticular exhibits some slight sculpturing.

The last stage we figure is 11.2 mm (fig. 5C). The ectopterygoid is now a long and massive bone that not only covers the pars autopalatina medially but also has dorsal and ventral flanges of bone that curve toward each other laterally, thus wrapping around a considerable part of the pars autopalatina. Posteroventrally the ectopterygoid almost reaches two pointed processes of the quadrate that extend anteriorly toward it. The posterior end of the quadrate bears a dorsal process of membrane bone that abuts an anteroventral process on the dorsal edge of the metapterygoid, but the bones remain separated by cartilage. All opercular bones except the subopercle are relatively larger and more extensively ornamented. A fifth spine is present at the lower end of the opercle. The preopercle shows some sculpturing and extends from the lateral flange of the hyomandibular anteriorly beyond the jaw joint and covers the anterodorsal part of the interopercle laterally. It thus covers the symplectic completely in lateral view. The sculpturing of the anguloarticular has intensified and that of the dentary has started to form.

ONTOGENY OF GILL ARCHES

We describe the gill arches of two developmental stages, a 4.3-mm larva and a 28-mm adult.

In the larval specimen (fig. 6A) each hyoid bar comprises a rectangular hypohyal cartilage and a rodlike ceratohyal cartilage. The anterior and posterior ceratohyal ossifications appear as thin perichondral lamellae, whereas the hypohyal cartilage shows no evidence of ossification. All six branchiostegal rays are already developed. The anterior two branchiostegals are thinner and shorter than the subsequent ones and they articulate with the anterior ceratohyal. The longer posterior four attach to the broad cartilaginous area that separates anterior and posterior ceratohyal. They curve around the opercular opening so that the distal tip of the posteriormost ray almost extends up to the dorsolateral corner of the operculum (see pl. 1E). The copula communis, within which the basihyal and basibranchials one through three will later ossify, is present as a continuous rod of cartilage. The anterior end of the copula ex-

pands laterally to form a conspicuous triangular plate, and posteriorly it tapers to a narrow rod that terminates between the third hypobranchials. The hypohyal and three hypobranchial cartilages (the third somewhat elongate) articulate along each side of the copula, and posteriorly, basibranchials four and five are present as two separate median cartilages. Basibranchial four lies between the medial ends of the fourth ceratobranchials, and basibranchial five lies between it and the anterior tips of the fifth ceratobranchials. The five ceratobranchials are elongate rods of cartilage with thin perichondral ossification at their midlengths. They decrease in length succesively from one through five, and all but the fifth, which bears a few small teeth on its dorsal surface, are edentate at this stage. There are four cartilaginous epibranchials. The first is a small short rod, the second and third are elongate and three times the length of the first, and the fourth is the largest with its medial end greatly expanded. Epibranchials two and three articulate with the anterior tip and midlateral portion of pharyngobranchial three, respectively. There is no fourth pharyngobranchial, and the expanded head of epibranchial four articulates with the dorsal surface of the fourth upper pharyngeal toothplate. The relatively robust and elongate third pharyngobranchial is ossified posteriorly and bears a few small conical teeth on its ventral surface, as does the smaller, fully ossified fourth upper pharyngeal toothplate.

The gill-arch skelton of the adult was described by Banister (1970), but we add some significant details not included in his description (fig. 6B). The dorsal and ventral hypohyals are ossified, as are the anterior and posterior ceratohyals. The dorsal hypohyal has a long posterodorsal extension that extends along half the length of the anterior ceratohyal and sutures with it dorsomedially. The anterior and posterior ceratohyals are separated by a narrow band of cartilage, and there are no bony lamellae or prongs extending across it, nor did we find the ankylosing of anterior and posterior ceratohyals described by Banister (1970). Copular ossification has produced the basihyal and three basibranchials. The anteriormost bone, the basihyal, is a very large, elongate element with a cartilag-
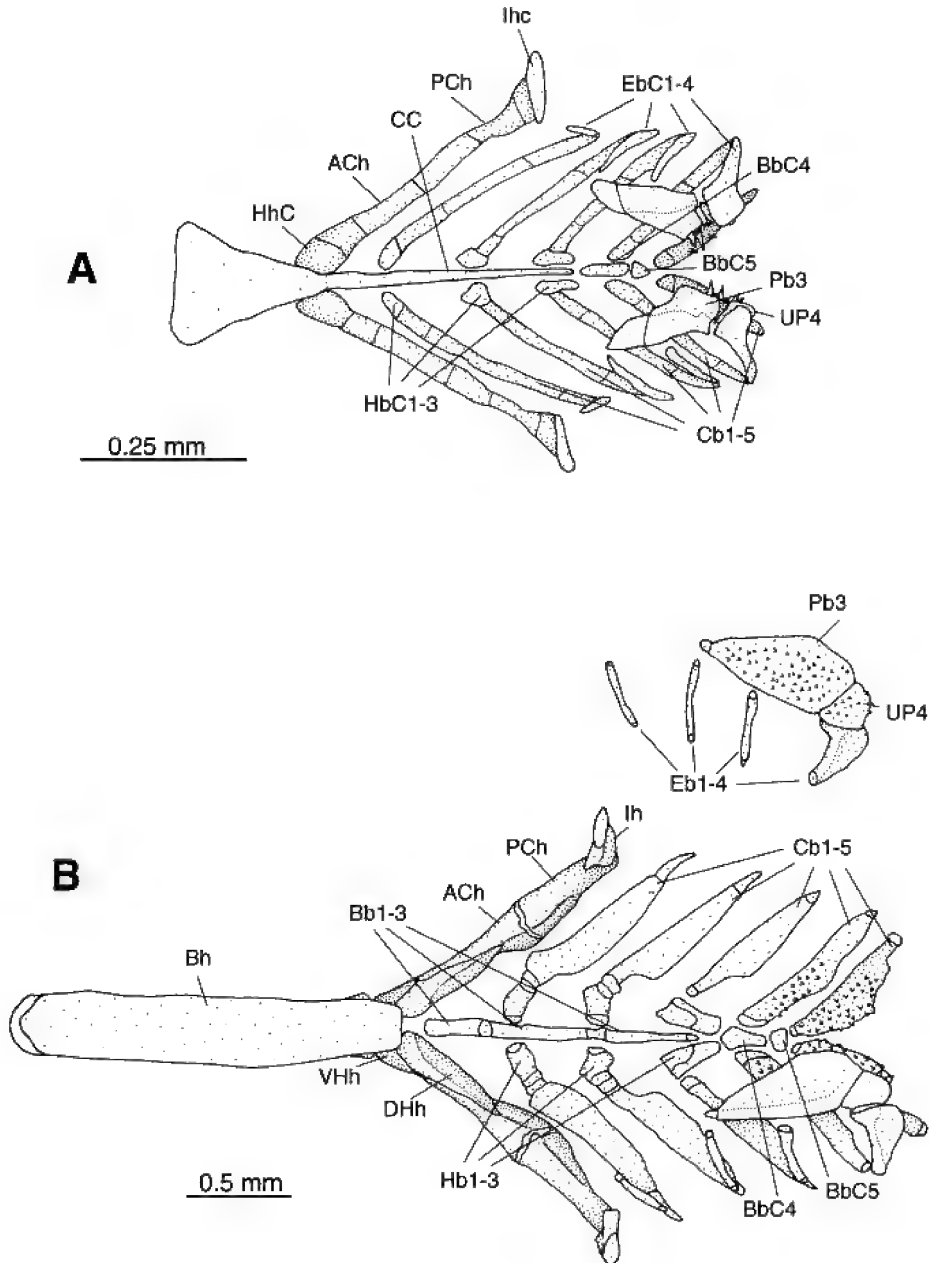
Fig. 6. *Indostomus paradoxus*. Developmental stages of hyoid and gill arches, dorsal view. **A.** 4.3 mm (USNM 366869). **B.** 28 mm (adult, USNM 366875), dorsal gill arches of right side in ventral view.

inous anterior tip, with no posterior cartilaginous connection to the first basibranchial. (This connection, however, is still present up to 11.2 mm but is lacking in our 16.6-mm specimen.) The three basibranchial ossifications are continuous with one another through cartilage. The cartilaginous posterior

tip of basibranchial three turns ventrally at the level of the third hypobranchials. Basibranchials four and five remain cartilaginous. The first two hypobranchials are short cylinders ossified perichondrally except at their medial and lateral tips; they articulate respectively at the anterior end of the second

basibranchial and at the cartilage joining basibranchials two and three. The third hypobranchial is more elongate and ossified only anteromedially; posteriorly it approaches (and even meets in one specimen) its contralateral member at the midline between the posterior end of the third and the anterior end of the fourth basibranchials.

The five ceratobranchials now have posterior laminar expansions and are roughly more equal in length. They differ much less in length among each other when compared to those of the larval stage. Ceratobranchials one and two bear long cartilaginous tips. Ceratobranchials four and five bear up to 20 and 30 teeth, respectively. (Teeth are still lacking on ceratobranchial four in our 11.2-mm specimen, but up to six teeth are present on that element in our 16.6-mm specimen.)

The four epibranchials are only slightly different in their shape and position. Epibranchial one is relatively longer and epibranchial four has a broad laminar flange posteriorly. The third pharyngobranchial and fourth upper pharyngeal toothplate are relatively larger and bear about 40 and 10 teeth, respectively. Pharyngobranchial four remains absent.

ONTOGENY OF SHOULDER GIRDLE

We describe five developmental stages of the shoulder girdle. At 4.3 mm (fig. 7A), the only ossification is the cleithrum, a long rod with several short processes, including a posteroventrally directed process near its ventral tip. The scapulocoracoid cartilage is attached to the posterior edge of the cleithrum at approximately midlength. A processus coracoideus projects posteroventrally from the body of the cartilage. The pars scapularis is not connected to the cleithrum but it has an anterodorsal process that approaches a posteroventral process from the cleithrum. The cartilage disc that supports the pectoral fin, termed the pectoral radial plate by Johnson and Brothers (1993), articulates with the posterior face of the scapulocoracoid cartilage and shows a longitudinal incisure.

In our 5.5-mm specimen (fig. 7B), the cleithrum is broader. Anterior to its dorsal end, the posttemporal and the supracleithrum appear as two small splintlike ossifications.

The anterodorsal process of the scapulocoracoid cartilage now attaches to the cleithrum, and the pectoral radial plate is relatively larger. The processus coracoideus is less prominent.

At 8.7 mm (fig. 7C), the cleithrum has a large posterior flange, and there is visible ornamentation on most of its lateral surface. The flange covers the base of the scapulocoracoid cartilage laterally, and its ventral part has a prominent ventral extension. The posttemporal is now much larger, roughly rectangular, and also shows some ornamentation. It is connected to the cleithrum by the relatively small, oblong, unornamented supracleithrum. The scapulocoracoid has fused with the pectoral radial plate. The posterior edge of the latter supports about 14 short fin rays. Dorsal to the longitudinal incisure of the now fused cartilaginous pectoral radial plate there are two probably anomalous small holes not seen in other specimens. The processus coracoideus is no longer recognizable as a separate projection. Two vertically oriented, styliform ossifications lie medial to the pectoral radial plate, with only their dorsal tips extending above it. They appear to be in series with ornamented lateral plate ossifications that form part of the body armor. The anteriormost of the two styliform ossifications approaches the cleithrum dorsally and most likely represents the dorsal postcleithrum. The more posterior of the two may be either the anteriormost lateral plate of the developing armor or the ventral postcleithrum. We are unable to decide unequivocally between these two options but favor the first because there is no other gasterosteiform with two postcleithra.

In our 11.2-mm specimen (fig. 8A), the cleithrum is farther expanded and more extensively sculptured. The posttemporal has a prominent anteroventral process that attaches to the exoccipital by ligament. A second process extends ventrally from its posterolateral edge, curving posteriorly to attach to the supracleithrum, which now exhibits minor sculpturing. The scapulocoracoid cartilage remains extensive, and the incisure in the fused pectoral radial plate is relatively smaller. The processus coracoideus is lacking. The uppermost end of the scapulocoracoid cartilage has two small foramina with a peri-
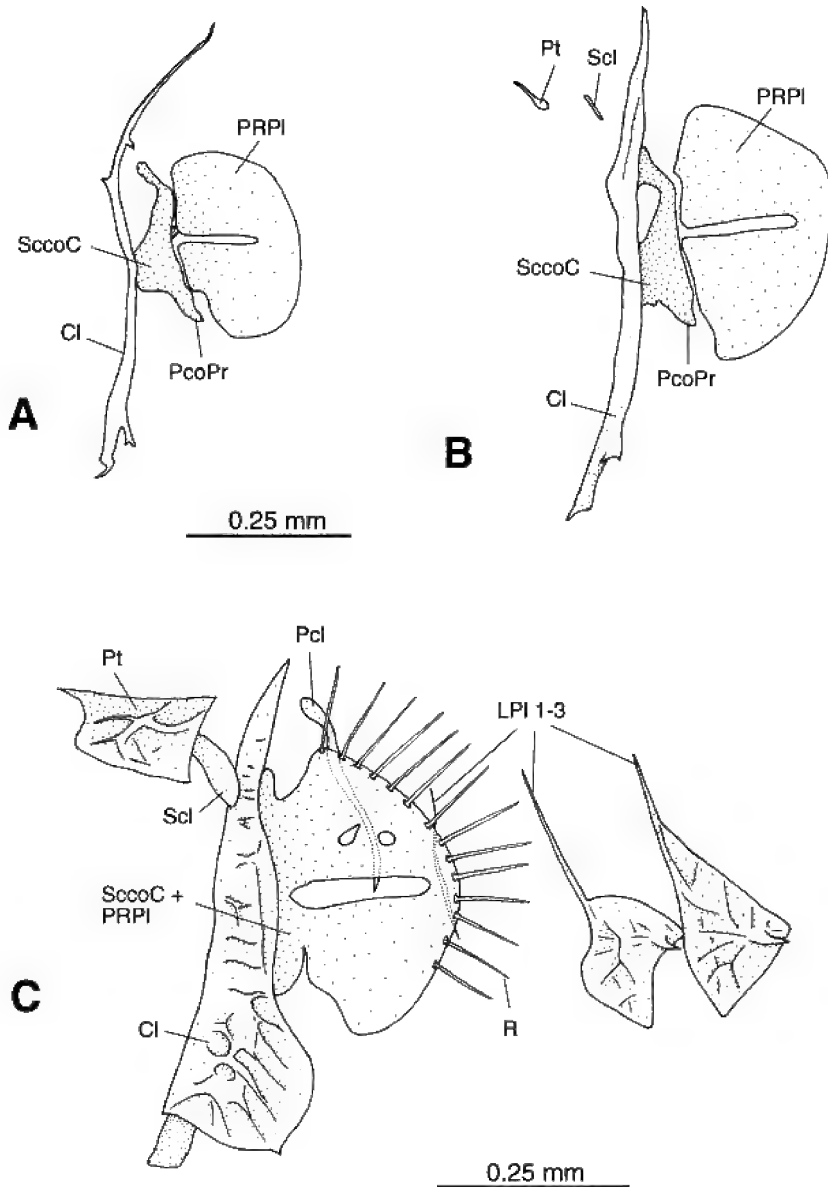
Fig. 7.   *Indostomus paradoxus* (USNM 366869). Ontogeny of pectoral girdle, lateral view. **A.** 4.3 mm. **B.** 5.5 mm. **C.** 8.7 mm.

chondral ossification, the scapula, surrounding the lower one completely and the upper one partly. Twenty-two pectoral fin rays are present. The now slightly ornamented postcleithrum is broader and longer and almost contacts the cleithrum dorsally. The succeeding element, the first lateral plate of the body armor, is also longer, broader, and slightly ornamented.

In the adult (32 mm), the cleithrum is much broader, and its posterior flange covers most of the scapulocoracoid and radials so that only their distal parts are visible in lateral view (fig. 8B). It also has a large anteromedial flange whose dorsomedial corner is tightly bound by a strong ligament to the tranverse process of the first vertebra (fig. 3D). The cleithrum and supracleithrum share
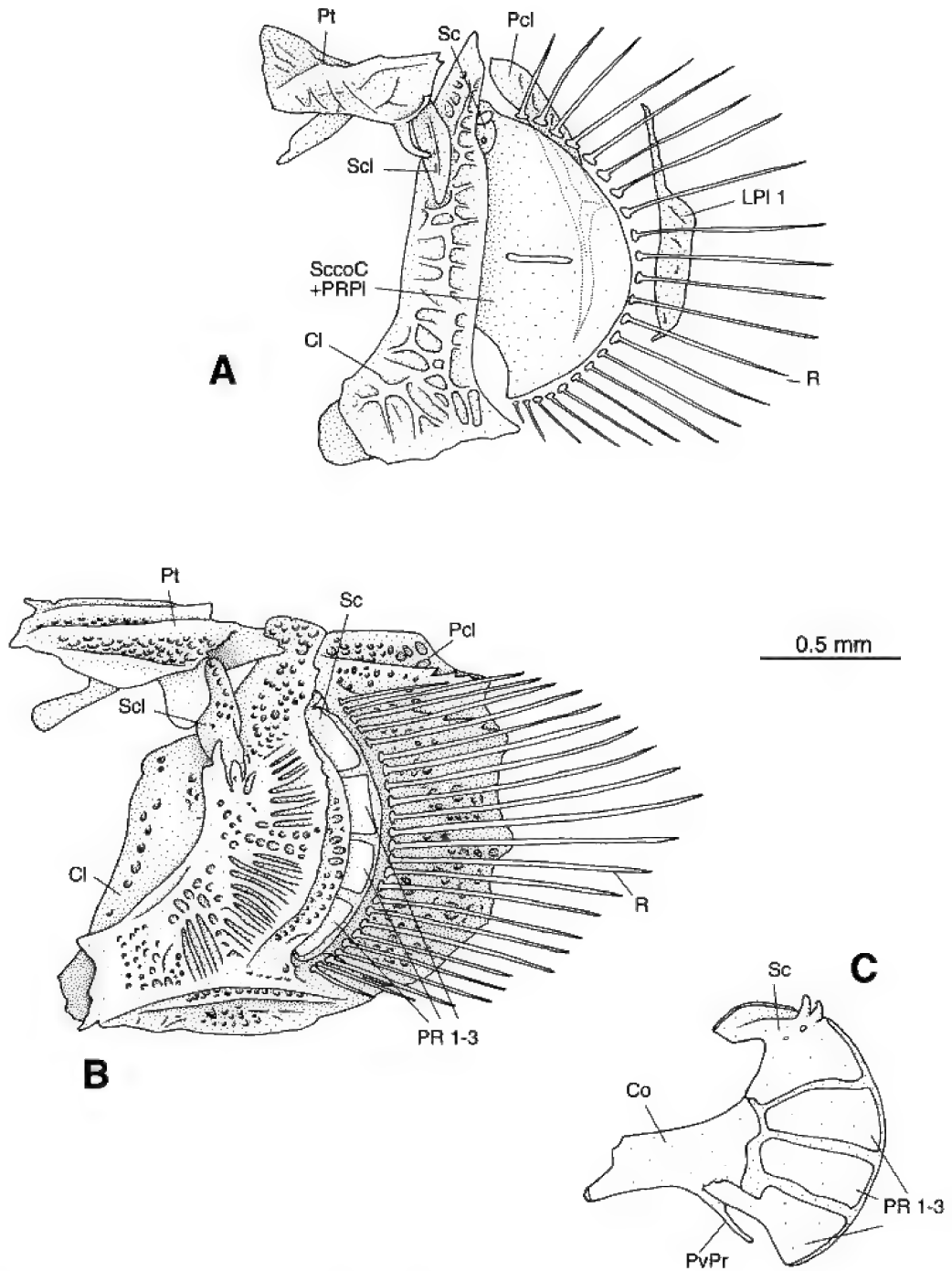
Fig. 8. *Indostomus paradoxus* (USNM 366869). Ontogeny of pectoral girdle, continued, lateral view. **A.** 11.2 mm. **B.** 32 mm. **C.** Scapulocoracoid and fused pectoral radial plate of same specimen removed.

an interdigitating suture. The posttemporal is platelike and integrated into the body armor. Its posteroventral process is broad and tightly bound to the supracleithrum. The postcleithrum now forms a large ornamented plate and at its dorsal and ventral tips is in tight contact with the cleithrum. The posterior edge of the postcleithrum overlaps the anterior part of the first lateral plate of the body armor. When removed from the cleithrum (fig. 8C), the ossifications of the scapulocoracoid and the radials can be identified. The scapula bears two short processes that are tightly connected to the cleithrum and postcleithrum. Anterior to these two processes the cartilaginous margin of a broad dorsal flange abuts the dorsomedial surface of the cleithrum. Ventral to the processes are two tiny foramina. Below the scapula there are three broad ossified radials. The radials remain connected by cartilage, indicating that they ossified within the continuous cartilage of the fused pectoral radial plate; that is, separate cartilaginous radials never form. The lowermost radial bears an anterodorsal process that is sutured to the lateral surface of the coracoid. There are 24 fin rays present. The coracoid is the largest ossification of the endoskeletal shoulder girdle. It bears a narrow fully ossified posteroventral process that approaches the ventromedial face of the cleithrum, and its anteroventral cartilaginous tip contacts the anteromedial margin of the cleitrum well dorsal to its ventral tip. The posteroventral process has no cartilaginous precursor and is developed in all adult specimens and our 16.6-mm juvenile, but is lacking in all earlier stages.

ONTOGENY OF BODY ARMOR

The body of the adult *Indostomus* is completely enclosed in a body armor whose individual plates have a conspicuous ornamentation essentially identical to that exhibited by all surface bones of the skull. We describe the ontogeny of this armor below.

In our ontogenetic series, evidence of the developing body armor first appears in a 3.5-mm specimen (pl. 2A). Preural vertebrae 3–9 possess lateral membranous outgrowths from the distal tips of the neural and hemal spines. On preural vertebrae 5–7 the lateral

outgrowths of the neural spines already bear a pair of posterolaterally directed short spinules.

We figure schematic representations of four ontogenetic stages (figs. 9–12; see also pl. 2). In the 5.5-mm specimen (fig. 9), the paired series of lateral plates consists of five ossifications (2–6) in the dermis (see also pl. 2B, C). They are not in contact with each other and the last four bear a short posteriorly directed spinule. The dorsal series begins behind the dorsal fin and consists of eight broad plates that represent expanded neural spines. All except the most posterior one have a pair of posteriorly directed spinules at the posterior angles. The ventral series also consists of eight broad plates arising from hemal spines. As in those of the dorsal series, the posterior angles of all but the last bear a short spinule (see pl. 2E). Although not included in figure 9, short and thin lateral expansions of the distal proximal-middle radials of the soft dorsal and the anal fin could be demonstrated at high magnification (250×) under the compound scope already in a 5.3-mm specimen (pl. 2D).

In the 6.8-mm stage (fig. 10), an additional pair of lateral plates (LPl 1) lies anterior to the anteriormost lateral plates of the 5.5-mm stage (fig. 9, LPl 2), and ventral to this pair, another pair, the pelvic plates, have formed at the anterior tips of the pelvic cartilages (see pl. 2H). The full complement of dorsal plates is developed now, but individual plates remain separate from one another. The first dorsal plate represents the laterally expanded distal tip of a spineless dorsal fin pterygiophore. The following five dorsal plates are clearly lateral expansions of the distal tips of spine bearing proximal-middle radials of the spinous dorsal fin pterygiophores, which lack distal radials. At this stage, only the posterior two proximal-middle radials bear fin spines (presumably in supernumerary association, see Discussion below). The next six plates are formed by lateral expansions of distal ends of proximal-middle radials of the pterygiophores that serially support the six dorsal fin soft rays, each of which embraces an associated distal radial. The first of those pterygiophores does not support a supernumerary spine at any stage in development. The remaining nine dorsal plates consist of expand-
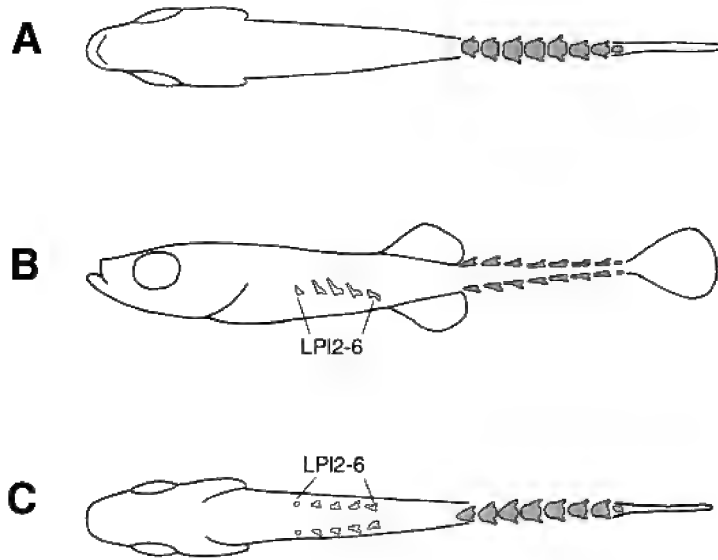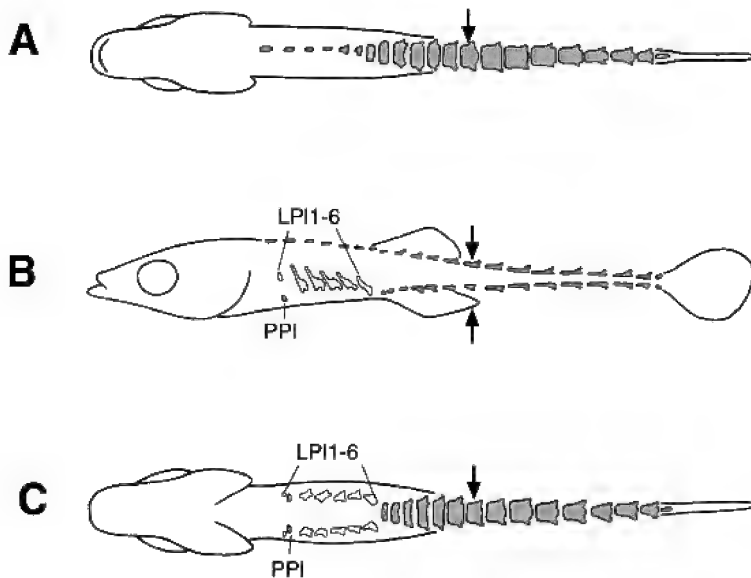
Fig. 9.   *Indostomus paradoxus*, 5.5 mm (USNM 366869). Schematic representation of body armor. **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. Exoskeletal components light gray, endoskeletal components darker gray.

ed neural spines. In the ventral series of plates we find a comparable situation. The anterior six plates are formed by lateral expansions of the distal tips of the proximal-middle radials of the pterygiophores that se-

rially support the six anal-fin soft rays (there are no anal-fin spines at any developmental stage), each of which embraces an associated distal radial, and the remaining nine plates are laterally expanded hemal spines. In the

Fig. 10.   *Indostomus paradoxus*, 6.8 mm (USNM 366869). Schematic representation of body armor. **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. Exoskeletal components light gray, endoskeletal components darker gray, arrows point to first plates originating from neural or hemal spines.
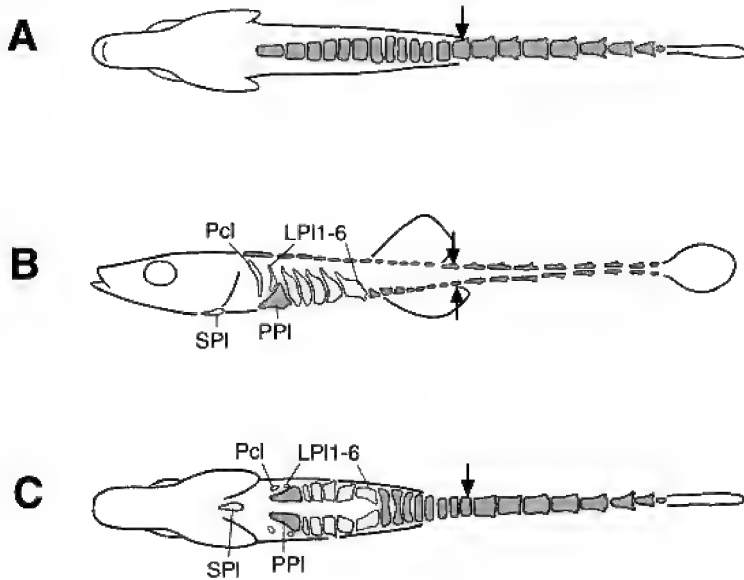
Fig. 11. *Indostomus paradoxus*, 11.2 mm (USNM 366869). Schematic representation of body armor. **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. Exoskeletal components light gray, endoskeletal components darker gray, arrows point to first plates originating from neural or hemal spines. Note that this specimen is unusual in having seven anal-fin rays and therefore seven ventral plates (instead of six) originating from pterygiophores.

ventral and posterior wall of the body cavity, in front of the anteriormost anal-fin pterygiophore and not visible externally, lies a separate shieldlike "anal" plate (not illustrated in fig. 10, but see pl. 2F).

In the 11.2-mm specimen (fig. 11), the anteriormost pair of plates in the lateral series is present so that there are now two plates in front of the original five plates of the 5.5-mm stage. As discussed above, we believe that its proximity to (and eventual articulation with) the cleithrum indicates that it is homologous with the dorsal postcleithrum of other acanthomorphs. All six lateral plates have grown dorsally and ventrally and have expanded laterally, although they remain separate. The pelvic plates are now large triangular bones. Anterior to the cleithral symphysis, an unpaired dermal sternal plate has formed in the ventral midline. All plates of both the dorsal and ventral series have expanded laterally but do not reach to the sides of the body.

The next stage we describe, not figured here, is 16.6 mm and closely resembles the adult stage, differing only in the following points. The lateral plates do not meet in the ventral midline, and their dorsal ends do not overlap the ventral margin of the dorsal plates. Only the anterior halves of the pelvic plates contact each other in the ventral midline. Finally, the dorsal and ventral plates that originate from the pterygiophores of the soft-dorsal and anal fins do not show the overlap present in the adult.

The body armor of the adult can be characterized as follows (fig. 12). In the dorsal midline a series of usually 21 plates completely covers the dorsum. The anteriormost plates are broad, approximately equally so, but posterior to the dorsal fin each becomes successsively narrower as the series extends posteriorly along the long, tapering caudal peduncle. There are seven plates anterior to the first dorsal soft ray. Of these, the anteriormost is spineless, and numbers 2–6 each bear a dorsal-fin spine. All dorsal plates curve around the body; numbers 1–6 stop at about the upper fourth of the body height, 7–13 reach approximately the lateral midline, and 14–21 fuse with the ventral plates to form a complete bony ring around the body. In lateral view there is a series of plates posterior to the cleithrum beginning with the
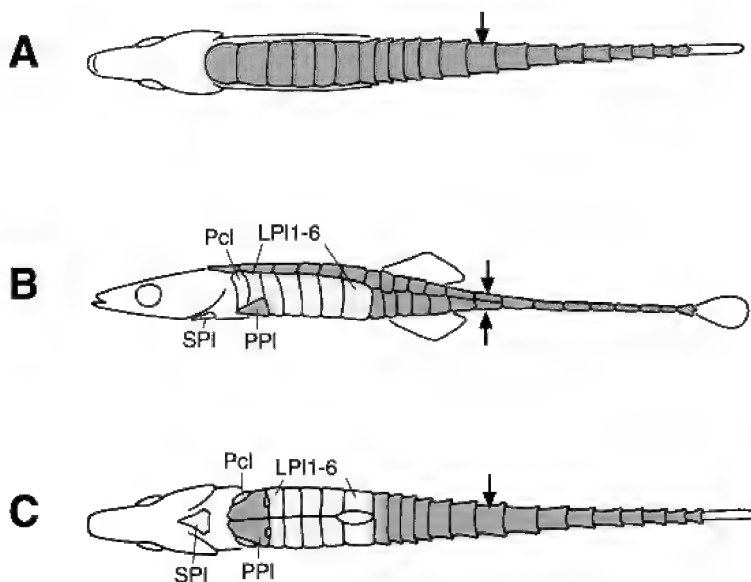
Fig. 12. *Indostomus paradoxus*, 28 mm (USNM 348212). Schematic representation of body armor. **A.** Dorsal view. **B.** Lateral view. **C.** Ventral view. Exoskeletal components light gray, endoskeletal components darker gray, arrows point to first plates originating from neural or hemal spines.

postcleithrum and followed by the six true lateral plates (1–6). Lateral plates 2–5 meet their counterparts in the ventral midline of the body. There is no lateral line or lateral line canal developed at any ontogenetic stage of *Indostomus*. The first dorsal plate contacts the cleithrum (not illustrated in fig. 12) and the postcleithral plate, and the second dorsal plate contacts lateral plates one and two. Dorsal plates 3–6 are associated with lateral plates 3–6. The last lateral plate (six) is broader than the others and contacts both dorsal plates six and seven. The six lateral plates are followed by seven ventral plates that curve up the sides of the body to meet their dorsal counterparts. Below the postcleithral and first lateral plates sits the pelvic plate, which meets its counterpart in the ventral midline. In ventral view we get the following picture. An unpaired sternal plate lies in the ventral midline anterior to the symphysis of the cleithra, and posterior to that symphysis lie the paired pelvic plates followed by lateral plates 2–5. The paired sixth lateral plates do not meet in the midventral midline along their whole width but enclose an unossified "window" for the openings of the anus and genital papilla.

In broad overview, then, we find that the body armor of *Indostomus* forms from two fundamentally different sources, the endoskeleton (i.e., parts of the axial skeleton, pelvic girdle, and pterygiophores) and the exoskeleton (i.e, dermal plates).

ONTOGENY OF PELVIC GIRDLE

The pelvic girdle is still completely lacking at 6.4 mm, and the first signs of it appear in our 6.8-mm specimen. Paired elongate and widely separated triangular cartilages have chondrified in the ventral part of the body at about the level of the third vertebra. The anterior end of each cartilage is already ossified perichondrally and bears irregular extensions of membrane bone. Two fin rays articulate with the caudolateral corner of each cartilage. The membranous areas of the pelvic fins have expanded farther in our 8.7-mm (pl. 2H) and 11.2-mm specimens to form the pelvic plates as described above. The cartilaginous part of the pelvic girdle is still clearly visible. There are four fin rays developed at 8.7 mm, five rays at 11.2 mm, but four rays in all our adult specimens.

ONTOGENY OF ARTICULATION OF
DORSAL-FIN SPINES

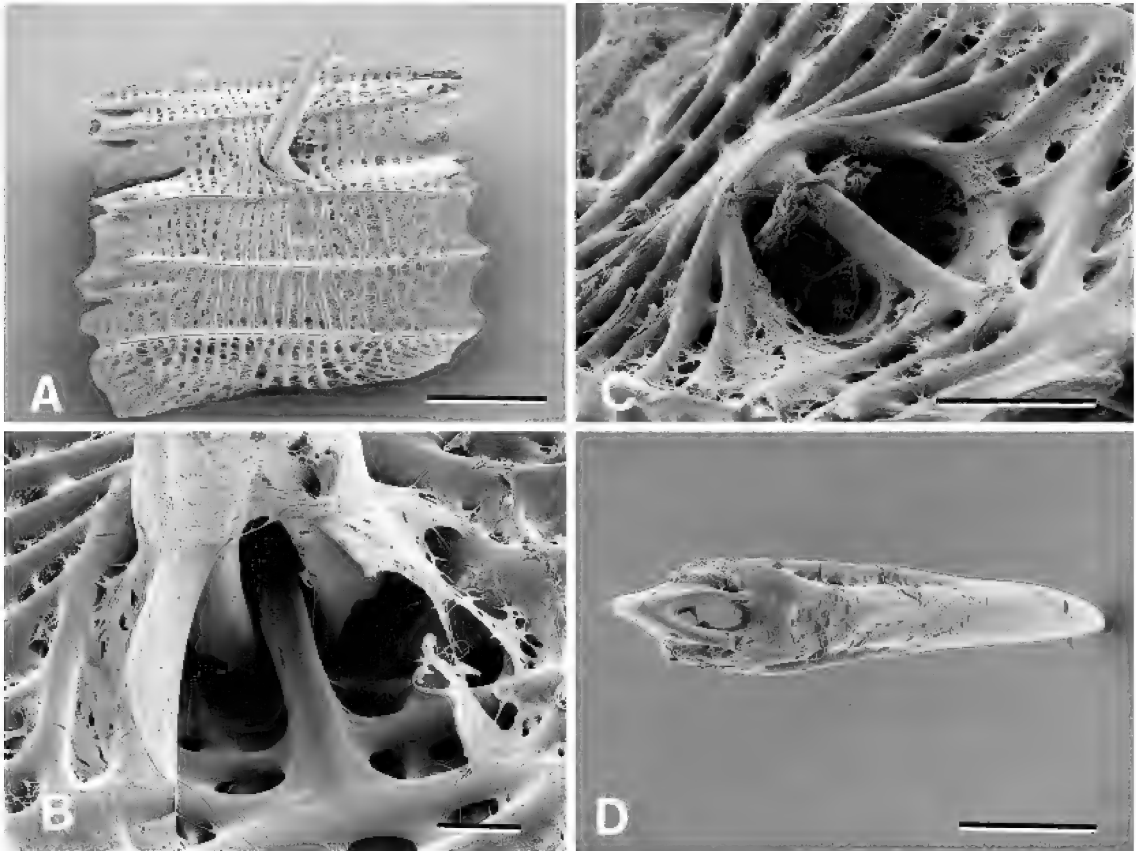Dorsal-fin spines and their supporting pterygiophores develop in a caudorostral gra-

Fig. 13. *Indostomus*. SEMs of dorsal-fin spine articulation. **A.** *I. paradoxus*, 32 mm (USNM 366875), fin spine with dorsal plate of body armor in dorsolateral view. **B.** Same specimen, close-up of articulation in posterior view. **C.** *I. spinosus*, 28 mm (USNM 366876), fin spine removed to expose articular bridge. **D.** Same specimen, isolated fin spine in anteroventral view, base of fin spine points to the left.

dient. We describe and figure a 5.3-mm specimen and the adult stage. The 5.3-mm stage has five pterygiophores chondrified with only the last two supporting fin spines (pl. 3D). The spines sit in supernumerary association with their open bases on the proximal-middle radials at about half of their length. All subsequent pterygiophores bear soft rays in serial association and have the usual complement of proximal-middle and distal radials.

In the adult *Indostomus* the distal ends of the proximal-middle radial of each fin spine-supporting pterygiophore form the conspicuously ornamented dorsal plates of the body armor (fig. 13). The fin spine articulates with a median ridge of bone on the dorsal surface of the plate (fig. 13B). This bony ridge ex-

tends between the anterior and the posterior rim of the articular groove that houses the most proximal part of the spine (fig. 13C). Processes extending medially from the anterolateral corners of the base of each spine fuse in the midline below the median bony ridge of the radial to enclose an opening resembling the eye of a needle; in this way, each spine is inextricably interlocked with its supporting radial (fig. 13D).

ONTOGENY OF CAUDAL FIN

We figure and describe four developmental stages. The first evidence of caudal-fin development appears in our 3.3-mm TL specimen (pl. 3E). All centra except PU3, PU2, and the terminal centrum are fully developed.
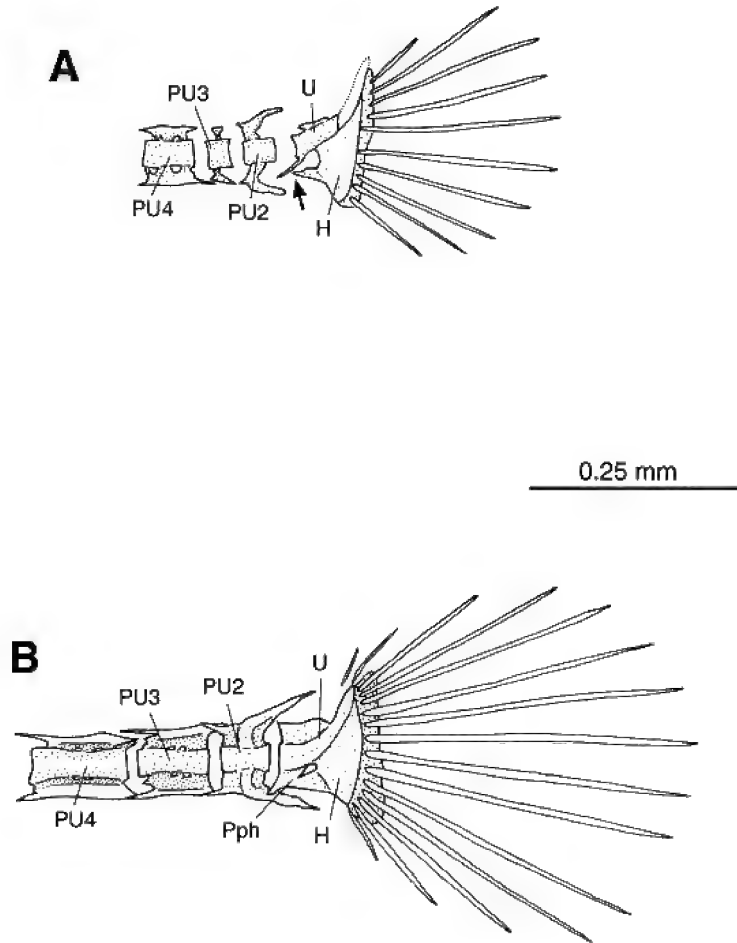
Fig. 14. *Indostomus paradoxus* (USNM 366869). Developmental stages of caudal fin, lateral view. **A.** 4.3 mm, arrow indicates incipient pseudoparhypural. **B.** 5.5 mm. Bone light gray, cartilage white.

PU2 consists of cartilaginous neural and hemal arches present as small paired knobs of cartilage above and below the chorda. There is a single elongate block of cartilage at the ventral side of the flexed chorda that represents a single hypural. There is no evidence suggesting it forms initially as several elements. Two caudal-fin rays articulate with it.

In our 3.8-mm specimen, PU3 is ossified and bears neural and hemal arches (pl. 3F). The terminal centrum has ossified and the single hypural has grown.

The caudal fin of the 4.3-mm stage has 10 fin rays that articulate basally with the single large hypural (fig. 14A, pl. 3G). The hypural is ossified basally and fused to the ural centrum. From the lower anterior edge of the

hypural a horizontal process of membrane bone projects anteriorly. The ural centrum is ossified around the lower part of the flexed chorda but does not extend to its posterodorsal end. The dorsal face of the centrum bears a low extension of membrane bone. At the anteroventral corner, paired pointed processes are directed anteroventrally, and with the approaching process from the hypural they form a foramen for the bifurcating caudal artery. PU2 bears a cartilaginously preformed full neural and hemal spine on each perichondrally ossified neural and hemal arch. In all vertebrae anterior to PU2 the respective neural and hemal arches and their respective spines develop directly in membrane bone, with no cartilaginous precursors. In the myo-

septa of the caudal musculature the first few intermuscular bones are ossified.

In the 5.5-mm specimen, 15 caudal-fin rays are developed (fig. 14B, pl. 3H). The ural centrum extends to the upper end of the chorda so that the hypural is fused to it along its entire length. The membranous dorsal lamina of the ural centrum is higher. The anteroventral processes of the centrum have fused to the horizontal anterior process of the hypural, thus forming a canal for the passage and a foramen for the exit of the caudal artery.

The adult condition differs little from that of the 5.5-mm specimen. The second preural centrum has developed the last ring of body armor that results from fusion of membranous lateral outgrowths of the neural and hemal spine of that centrum. This ring covers most of the ural centrum and hypural and bears on its caudal border two lateral spinules, and one dorsal and one ventral spinule. The hypural supports 12 principal caudal rays of which 10 bifurcate distally.

REMARKS ON FORMATION OF BONY NEURAL AND HEMAL CANALS

Indostomus usually has 21 preural vertebrae, of which 9 are abdominal and 12 are caudal. All centra are somewhat elongate with long bony canals enclosing the neural and/or hemal canals. These canal-like structures possess interdigitating processes and were considered neural and hemal arches by Banister (1970). We find that, except on PU2 (see above), all centra and neural and hemal arches develop in membrane bone without cartilaginous precursors. Our 3.8-mm specimen (with 22 preural vertebrae) has all centra fully developed except PU2, which has cartilaginous rudiments of neural and hemal arches (pl. 3F); there are also neural arches on vertebrae 1–4 and 11–21 (= PU13–PU3) and hemal arches on vertebrae 10–21 (= PU14–PU3). All neural and hemal arches are situated toward the anterior end of the vertebrae. The centra of PU4 and PU5 have very thin struts of bone at their caudal ends, being modified postzygapophyses (pl. 3F). The subsequent ontogeny is as follows: the modified dorsal postzygapophyses develop in a caudorostral direction on all vertebrae except

PU2; ventral postzygapophyses develop likewise in a caudorostral direction on all caudal vertebrae except PU2. Ventral and dorsal postzygapophyses then grow distally, and at about the same time neural and hemal arches develop horizontal caudal extensions at their distal tips (pl. 3D). Eventually, caudal extensions of neural arches (most likely neural spines) and dorsal postzygapophyses, as well as caudal extensions of hemal arches (most likely hemal spines) and ventral postzygapophyses, contact each other and fuse in the dorsal midline. Later also, the unossified area between the bases of the arches and the postzygapophyses ossifies to some extent and thus the elongate bony neural and hemal canals of the adult fish are formed (fig. 3D, H). In addition to small openings in the wall of the canal, only a pair of large lateral foramina remains at about midlength of the neural arches and represents the former gap between the latter and the dorsal postzygapophyses (fig. 3H). Ossification of the space between hemal arches and ventral postzygapophyses is less complete, and usually three pairs of larger foramina remain in the adult.

DISCUSSION

Since its original description the systematic position of *Indostomus* has been highly controversial, but the taxon has been aligned most frequently with various members of the Gasterosteiformes. It was thought by Prashad and Mukerji (1929: 219) to be "closely allied to the families Solenostomidae and Syngnathidae," whereas Bolin (1936: 423) claimed that "the Aulorhynchidae and Aulostomidae are by far most similar to the Indostomidae." Banister (1970: 204), who studied the osteology of *Indostomus* in more detail, rejected a close relationship with gasterosteiforms and suggested that "the order Indostomiformes be placed within the superorder Paracanthopterygii and probably near the Gobiesociformes." Fraser (1972: 240) pointed out that Banister's arguments for removal of *Indostomus* from the Gasterosteiformes were "negative (loss) characters and thus not very satisfying." In his study of the relationships of the sea moths, family Pegasidae, Pietsch (1978) also rejected Banister's hypothesis. Although he did not examine the

osteology of *Indostomus*, Pietsch (1987: 527–528) listed a number of specializations that *Indostomus* shares with Pegasidae and/ or more inclusive groups of gasterosteiform taxa and concluded "that the Indostomidae should be returned to the Gasterosteiformes, but that the specific relationships of the family within the order must await further investigation." Johnson and Patterson (1993: 577) presented additional evidence that led them to conclude that "*Indostomus* belongs in Pietsch's (1978) Syngnatha" and to infer that within that group it is the sister group of the Pegasidae. In his unpublished dissertation on gasterosteiform relationships, Orr (1995) argued against any relationship between *Indostomus* and Gasterosteiforms, and, although he did not include it in his formal cladistic analysis, he recommended its exclusion from the order. These disparate hypotheses about the phylogenetic position of *Indostomus* emanate from its highly derived adult anatomy and depend, in part, on the authors' different propositions about the identity of certain bones and the homology of certain features of the skeleton. Our study of the skeletal development of *Indostomus* facilitates the resolution of some of these homology problems, and below we treat them in order of their taxonomic inclusiveness.

CAUDAL SKELETON

Johnson and Patterson (1993: 579) proposed seven derived characters supporting monophyly of the Gasterosteiformes (including *Indostomus*). One of those involves several derived features of the caudal skeleton and was stated as follows: "The caudal skeleton includes a full neural spine on PU2; HPU2 and HPU3 fused to their centra; and the parhypural and five hypurals fused with each other and with the terminal centrum." Our study of the ontogeny of the caudal fin of *Indostomus* indicates that a true endochondral parhypural never forms. There is only one large cartilaginous hypural present and it is not pierced in early stages by the caudal artery. A separate parhypural does not form. Later in development three processes of membrane bone develop, a pair of processes from the terminal centrum and an unpaired one from the anteroventral face of the

hypural. These meet later in ontogeny and fuse together, leaving a foramen on each side of the hypural for the passage of the caudal artery. This formation thus mimics the presence of a parhypural and we refer to it as the pseudoparhypural. Thus, at least for *Indostomus*, the portion of Johnson and Patterson's caudal skeleton character that reads "parhypural and five hypurals fused with each other and with the terminal centrum" should be restated as "hypural plate develops as a single block of cartilage, which fuses to terminal centrum, both giving rise to outgrowths of membrane bone that form a pseudoparhypural."

Detailed ontogeny of the caudal skeleton is unknown for most gasterosteiforms, and composition of the caudal skeleton has thus been inferred from the adult state. The thin, laminar nature of the "parhypural" in other gasterosteoids (hypoptychids, aulorhynchids, and gasterosteids) may suggest that this element also is a pseudoparhypural, but developmental data are lacking for most taxa. Our ontogenetic series of *Gasterosteus* and *Aulorhynchus* demonstrate that the parhypural forms as a separate cartilage that later in ontogeny fuses with the lowermost hypural. In syngnathoids, the situation is more complex and variable, and we also lack detailed ontogenetic information on all taxa. For example, the parhypural clearly has an endochondral component in *Aulostomus*, where it is fused only at its base to the lower hypural and the terminal centrum, and in centriscids, where it is completely autogenous. In syngnathids and macroramphosids, on the other hand, it appears completely incorporated into the hypural plate, as in gasterosteoids. Needless to say, detailed skeletal ontogenetic studies of many more gasterosteiforms are needed before we can accurately delineate homologous character states within the order.

Beyond this, elucidation of hypural plate formation and discovery of a pseudoparhypural in *Indostomus* demonstrate the importance of ontogenetic information in establishing homologies and delineating character states in the caudal skeleton of fishes. There are numerous cases among teleosts in which fusion of caudal-fin elements is assumed without having been demonstrated. Such cases of assumed fusion of hypurals can be

found in Fujita (1990), who labeled elements of the caudal skeleton accordingly. This "fusion" then may be used in phylogenetic discussions as a character state. As we have shown above for the caudal fin of *Indostomus*, assuming fusion of elements from the adult state without having demonstrated their actual fusion during ontogeny can be misleading, and this again illustrates the importance of ontogenetic data to properly define characters used for phylogenetic reconstructions. It also adds additional information by testing the similarity of apparently identical adult characters through the study of their ontogeny. Adding the ontogenetic dimension to characters of the adult thus delineates and defines characters in a more precise way by enabling one to distinguish as different character states those similar adult states that differ in their ontogeny. For the sake of clarity we note here that we do not claim that differences in ontogeny unequivocally imply that nonhomologous states are involved.

There are numerous examples in the vertebrate literature in which a single element in a more derived taxon of a monophyletic group occupies the same space as two (or more) elements in more basal taxa. There are two interpretations of this finding. (1) The more derived taxon has lost one of the elements. (2) In the more derived taxon the two elements have fused into one. These two alternatives can be tested easily with ontogeny. If we find only one element developing, then case no. 1 applies; if there are two (or more) elements developing that fuse during ontogeny, then case no. 2 applies. The distinguishing power of ontogenetic studies, however, seems to fail in the case of phylogenetic fusion or fusion *ab initio* (sensu Patterson, 1975, 1977); for example, if the single hypural plate of *Indostomus* were considered the result of phylogenetic fusion of the parhypural and five hypurals. According to Patterson (1977: 93) phylogenetic fusion between two bones "requires that in successive ontogenies the two ossification centers should move progressively closer to each other until they are coincident, so that only one bone arises in ontogeny." We would need to assume an analogous mechanism for structures that are preformed in cartilage (as with hypurals) and that have fused already at the car-

tilaginous state (i.e., centers of chondrification becoming coincident). Patterson (1977) knew of no thoroughly documented examples of phylogenetic fusion between two dermal bones or two cartilage bones. Similarly, we know of no documented cases of chondrification centers becoming coincident in phylogeny. We doubt that such information is obtainable in theory and question the scientific integrity of such a hypothesis, because phylogenetic coincidence of chondrification centers is not a testable hypothesis. We therefore suggest that the only reasonable approach is the test of ontogenetic fusion as outlined above, and, in this study, we consider fusion between two or more bones to have occurred only if ontogenetic fusion is demonstrable (see paragraphs below on nasals, ectopterygoid, and parietal).

DORSAL-FIN SPINES

Another character cited by Johnson and Patterson (1993: 579) as a synapomorphy of gasterosteiforms is: "The dorsal fin spines, when present, are separate (isolated), not joined by membrane, and articulate at or posterior to the midpoint of the protracted dorsal surface of the pterygiophore." They also noted that gasterosteiforms share with most other smegmamorphs the absence of distal radials on spine-bearing dorsal pterygiophores (Johnson and Patterson, 1993: 580, table 2).

Our observations of the development of the dorsal fin in *Indostomus* agree with the conditions described above. Only the proximal-middle portions of the spine-bearing dorsal pterygiophores develop; distal radials are never present. Each dorsal-fin spine develops an articulation with the dorsal surface of a proximal-middle radial about midway along its length. The position of the spine on each pterygiophore and the absence of distal radials suggest that these spines are in supernumerary, as opposed to serial, association with their supporting pterygiophores; this is borne out by the fact that their position and articulation on the pterygiophores is identical to those of *Spinachia* and *Aulorhynchus* where the evidence for supernumerary association is unequivocal (see below). Our examination of other gasterosteiforms also confirms the conclusions of Johnson and Pat-

terson (1993). They all lack distal radials associated with the spinous dorsal pterygiophores, and in all gasterosteoids (except *Hypoptychus*, which lacks spines) the open bases of the fin spines articulate directly with a median bony ridge on the dorsal surface of the proximal-middle radials. The base of the fin spine in *Indostomus* is also open initially (still open in our 8.7-mm specimen) and articulates with a bony ridge of the radial but eventually (our 11.2-mm specimen) closes below the ridge and thus resembles the eye of a needle in the adult. Banister's (1970: fig. 2) account of the dorsal-fin spine articulation in *Indostomus* is misleading. He figured an anteriorly directed, distally pointed prong with which the spine base articulates. This figure led Orr (1995) to question the similarity of the spine articulation between *Indostomus* and other gasterosteiforms. As described above, however, articulation is with a median bony bridge as in other gasterosteiforms. Information on spinous dorsal-fin development is needed for gasterosteoids, but, again, it is clear that the spines are in supernumerary association with the proximal-middle radials that support them. Our developmental series of *Gasterosteus* shows lack of distal radials in the spinous dorsal fin in all developmental stages (e.g., 10.3-mm *G. aculeatus*, pl. 3C). Among syngnathoids, dorsal spines are variously present or absent and, in some macroramphosids, may fuse with the supporting radial. A condition resembling that found in gasterosteoids appears to occur in adult aulostomids, but again ontogenetic information is lacking. As for the soft dorsal fin, our observations indicate that in all gasterosteiforms the dorsal-fin soft rays embrace the distal radials of their serially associated pterygiophores, as is typical for teleosts.

One of us (RB) observed a dorsal-fin spine-radial articulation similar to that of gasterosteoids in developmental stages of the smegmamorph mastacembelid, *Macrognathus pancalus* (pl. 3B)—only proximal-middle radials form in the spinous part of the dorsal fin, and the spines articulate directly with these in supernumerary association.

OCCIPITAL ARTICULATION

Orr (1995) recognized five synapomorphies of Gasterosteiformes, from which he excluded *Hypoptychus* and *Indostomus*. One of them concerns the articulation between the occiput and the first vertebra. For acanthomorphs the plesiomorphic condition is to have a tripartite articulation. In addition to the more primitive articulation between the basioccipital and the first centrum, the latter possesses an "anterior surface bearing distinct facets that articulate with the exoccipital condyles" (Johnson and Patterson, 1993). We agree with Orr (1995) that Gasterosteiformes lack such a tripartite occipital condyle, and the posterior processes of the exoccipitals are expanded. A tripartite occipital condyle is also lacking in *Indostomus*. In early stages there is only the articulation between the basioccipital and the first centrum. Later, two horizontal membrane bone processes develop from the exoccipitals and gain contact with expanded anterior flanges of the transverse process of the first vertebra. Although the adult condition of the occipital articulation in *Indostomus* is unique among gasterosteiforms and represents an autapomorphy of this genus, this taxon apparently shares with other gasterosteiforms a unique ontogeny of the occipital articulation. The regular acanthomorph tripartite condyle originates from cartilaginously preformed condyles on the exoccipital bones that later in development articulate with condyles on the first vertebra that are also preformed in cartilage, as our developmental stages of *Morone* (uncat.) demonstrate. *Indostomus* and other gasterosteiforms lack the cartilaginously preformed condyles on the exoccipitals and on the first vertebra. We encountered horizontal membrane bone processes on the exoccipitals similar to those of *Indostomus* in our developmental stages of *Gasterosteus* and *Spinachia*. These, however, fail to contact the transverse processes of the first vertebra. Later in development they are incorporated into the developing lateral flanges of membrane bone on the exoccipitals of the adult and thus become less conspicuous.

ONTOGENY OF PECTORAL GIRDLE

Our results of the ontogeny of the pectoral girdle in *Indostomus* have revealed a character complex that may be of phylogentic significance. In the adult fish all three radials

remain connected by cartilage to each other and to the scapula and coracoid, suggesting that they ossified within the continuous fin-supporting cartilage plate; that is, separate cartilaginous radials never form. Usually in teleosts the cartilage plate that chondrifies during early ontogeny and that supports the pectoral fin remains separate from the scapulocoracoid cartilage and becomes fragmented into distinct cartilaginous radials that later ossify (for different percomorphs, see, e.g., Potthoff et al., 1984, 1987, 1988; Potthoff and Tellock, 1993; for zebrafish, see Grandel and Schulte-Merker, 1998). Thus, fragmentation of the separate cartilage plate into radials that are circular in cross section typically precedes their ossification. The result is a perichondral ossification that surrounds individual radials completely. This is unlike the situation we describe for *Indostomus* in which the pectoral radial plate fuses to the scapulocoracoid cartilage and ossification of each radial consists of two separate perichondral laminae of bone, one on the lateral and one on the medial side of the continuous cartilage plate.

Detailed information on the development of the pectoral-fin skeleton in other gasterosteiform fishes is still lacking. However, we found ossified laminar radials that are still connected through cartilage to each other and to the scapulocoracoid in *Gasterosteus*, *Culaea*, *Apeltes*, *Pungitius*, *Spinachia*, *Aulorhynchus*, *Aulichthys*, and *Hypoptychus*, implying that in all gasterosteoids, as in *Indostomus*, the pectoral radial plate fuses to the scapulocoracoid, fragmentation of that cartilage plate never occurs, and ossification of the radials occurs within the intact plate.

BODY ARMOR

Berg (1958) noted that the body armature of the Indostomidae is "remarkably like that of the Syngnathidae." Pietsch (1978: 527) listed this as one of eight specializations shared by the Indostomidae and Pegasidae, describing it as follows: "the elongate head and trunk are encased by bony plates and the tail is encircled by bony rings (as in the Syngnatha)." Johnson and Patterson (1993: 577) again referred to Pietsch's character as "remarkable similarity between the body ar-

mor of *Indostomus* and the syngnathids." With the ontogenetic series of *Indostomus* at hand, we are able to provide a detailed account of its body armor and a comparison with that of other gasterosteiforms. As described above, the body armor of *Indostomus* comprises the following components: (1) an unpaired row of dorsal plates—the first plate forms from the anteriormost expanded rayless pterygiophore, the following five plates from the expanded pterygiophores supporting the five supernumerary fin spines, the following six plates from the expanded pterygiophores serially supporting the soft rays of the dorsal fin, and the last nine plates from expanded neural spines of preural vertebrae; (2) a pair of plates originating from expanded cleithra; (3) a pair of plates representing expanded dorsal postcleithra; (4) a series of six pairs of dermal lateral plates; (5) an unpaired sternal plate in front of the cleithral symphysis; (6) paired pelvic plates arising from the pelvic-fin cartilages; (7) an unpaired series of ventral plates—the first six plates develop from expanded pterygiophores of the anal fin, and the remaining nine plates from expanded hemal spines of preural vertebrae. Below, we describe the body armor arrangements in several members of the Syngnatha and in gasterosteoids for purposes of comparison with that of *Indostomus* (see figs. 15–18 for schematic representations of these).

The putatively basalmost syngnathoids, the Aulostomidae and Fistulariidae (Orr, 1995), have no body armor. *Aulostomus* has peripheral ctenoid scales (Roberts, 1993) and *Fistularia* possesses small osseous spinules in the skin. Depending on the species, these can be well developed in all stages, as in *F. petimba*, or present only in juveniles and not visible in the adult, as in *F. tabacaria* and *F. commersonii* (Fritzsche, 1976).

The body armor of centriscids was described in detail by Jungersen (1908), and points pertinent to the discussion are repeated here. In *Centriscus* (fig. 15A), the body armor consists of dorsal and ventral components. The dorsal component comprises two bilateral series of five plates each. Four of the five paired plates of the dorsalmost of these two series meet in the midline, and an additional unpaired sixth plate separates the
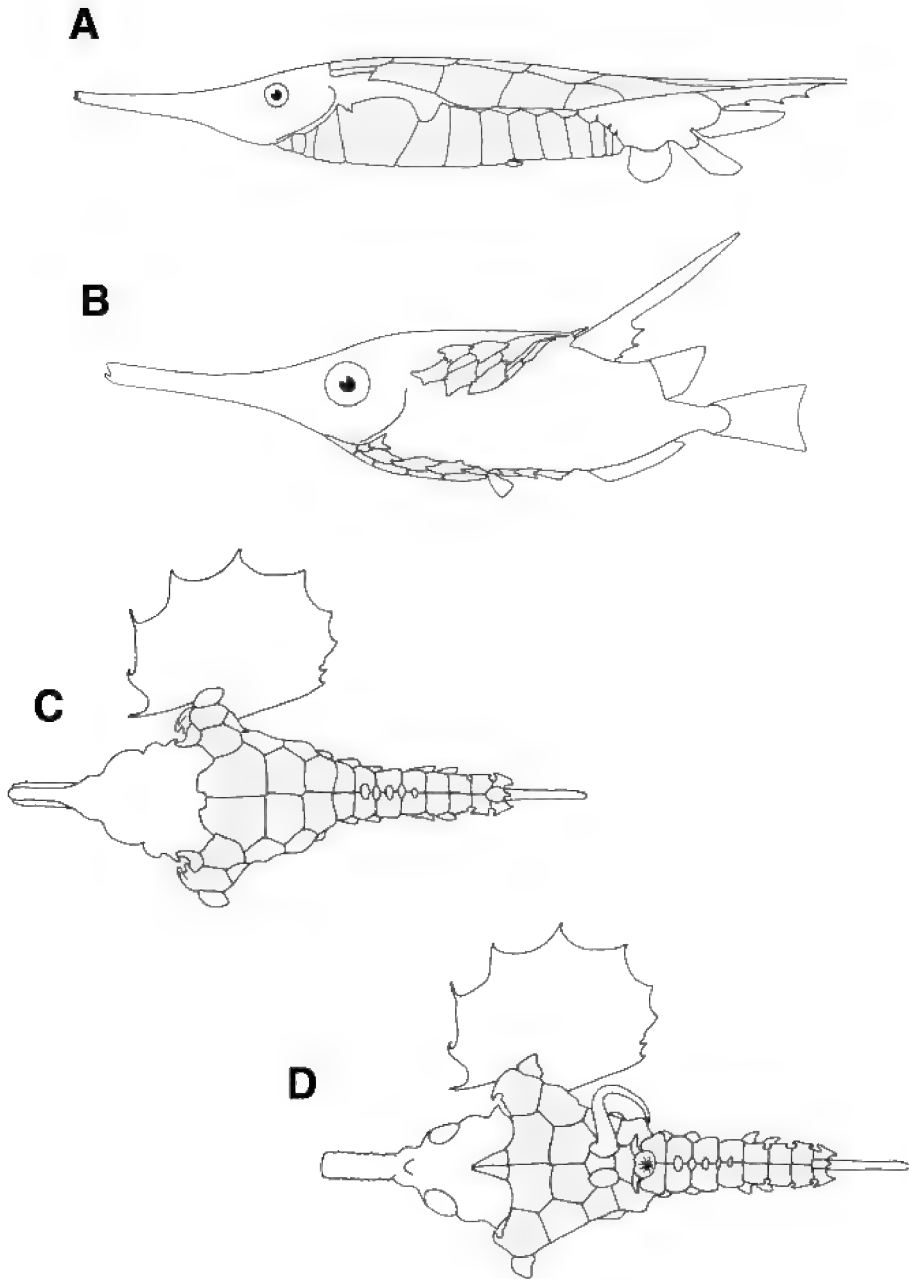
Fig. 15.   Schematic representation of body armor of adult syngnathoids. **A.** *Centriscus scutatus*, ca. 90 mm, lateral view. **B.** *Macroramphosus scolopax*, ca. 90 mm, lateral view. **C.** *Eurypegasus draconis*, based on two specimens (49 mm, 25 mm), dorsal view. **D.** Ventral view. A and B after Jungersen (1908), C and D after Rendahl (1930).

fifth plates in the midline and extends well posteriorly to form a roof for the dorsal fin. The five paired plates of the ventralmost of these two dorsal series lie below and contact the ventral margins of the five paired plates of the dorsalmost series. The ventral component of the armor usually comprises 14 unpaired plates that reach up the sides of the

body and may contact some or all of the five paired plates of the ventralmost of the two dorsal series.

In *Macroramphosus* (fig. 15B), the body armor also consists of dorsal and ventral components, and again the dorsal component comprises two bilateral series of plates. The dorsalmost series consists of three plates that do not meet in the dorsal midline; the ventralmost of the two dorsal series has five plates of which the first three contact the ventral ends of the upper series. The ventral component of the armor is represented by a series of nine paired plates, one on each side of the lower edge of the belly and an unpaired ventromedian series of six plates extending from the isthmus to the anus.

The body armor of pegasids was described in detail by Rendahl (1930). In this family, the body is completely enclosed in dermal bony plates. Our description and schematic representation is based on *Eurypegasus draconis* (fig. 15C, D). There is a series of 11 paired dorsal (scuta dorsalia and caudodorsalia of Rendahl) and 12 paired ventral plates (scuta pectoralia, ventralia, analia, and caudoventralia of Rendahl) extending from the skull region to the caudal fin. In the abdominal area a series of three paired dorsolateral (scuta dorsolateralia of Rendahl) and a series of four paired ventrolateral plates (scuta ventrolateralia of Rendahl) are present. Several unpaired plates occur in the ventral region between the pelvic fins (scutum interventrale of Rendahl), in front of the anus (scutum praeanale of Rendahl), and in front of the dorsal and ventral bases of the caudal fin (scutum terminale dorsale et ventrale of Rendahl). Additional plates also cover the dorsal and ventral bases of the large pectoral fins (scuta extralateralia of Rendahl). Three to four lateral plates (scuta caudolateralia of Rendahl) are formed on both sides of the caudal peduncle wedged in between the dorsal and ventral plates.

In *Solenostomus* (fig. 16A) the dorsal and ventral surfaces of the body in front of the dorsal and anal fins are covered by a series of five dorsal and four ventral median plates. Several lateral series of stellate plates are developed on both sides of the trunk and tail region. All plates in *Solenostomus* are ossifications in the dermis and thus belong to the

exoskeleton. They do not cover the whole body but rather leave large portions of the skin without ossification.

The body of pipefishes is completely enclosed in bony plates that form a rigid armor. The arrangement of the different plates varies among the species. A pattern encountered in *Syngnathus typhle* can be described as follows (fig. 16B–D). There are three bilateral series of plates, one dorsal whose members meet in the dorsal midline, one lateral, and one lateroventral whose members do not meet in the ventral midline. In addition, there is one series of unpaired ventral plates. The spaces between these series of larger plates are filled by series of smaller plates, one median unpaired row along the back, two paired rows along the sides, and one paired row along the ventrolateral aspect of the body. There may be one (*Nerophis ophidion*) or two (*Syngnathus typhle*) large median plates in the dorsal midline directly posterior to the skull, termed nuchal plates by Jungersen (1910), who believed them to be expanded pterygiophores. Their ontogeny, however, is not known. All body plates of syngnathids, except possibly the nuchal plates, ossify in the dermis and therefore belong to the exoskeleton.

The body armor of aulorhynchids and gasterosteids was briefly decribed and illustrated by Nelson (1971). In gasterosteids it consists of a dorsal unpaired row, lateral paired rows, an unpaired ventral row, and paired pelvic plates. We illustrate the plate arrangement in *Spinachia spinachia* (fig. 17A–C) and *Gasterosteus aculeatus* (fig. 17D). The plates of the dorsal series in *Spinachia* arise over most of the body's length from expansions of the proximal-middle radials as follows, rostrocaudally: 2 anterior plates from rayless pterygiophores, 15 plates from pterygiophores supporting the 15 dorsal spines supernumerarily, the last of which also serially supports the first dorsal soft ray (thus corroborating supernumerary association of all dorsal spines with their supporting pterygiophores), 5 plates from pterygiophores serially supporting the remaining five dorsal soft rays, 10 plates from rayless pterygiophores, and the remaining 8 plates from expanded neural spines. The paired lateral series consists of 41 plates bearing the lateral-line canal. There
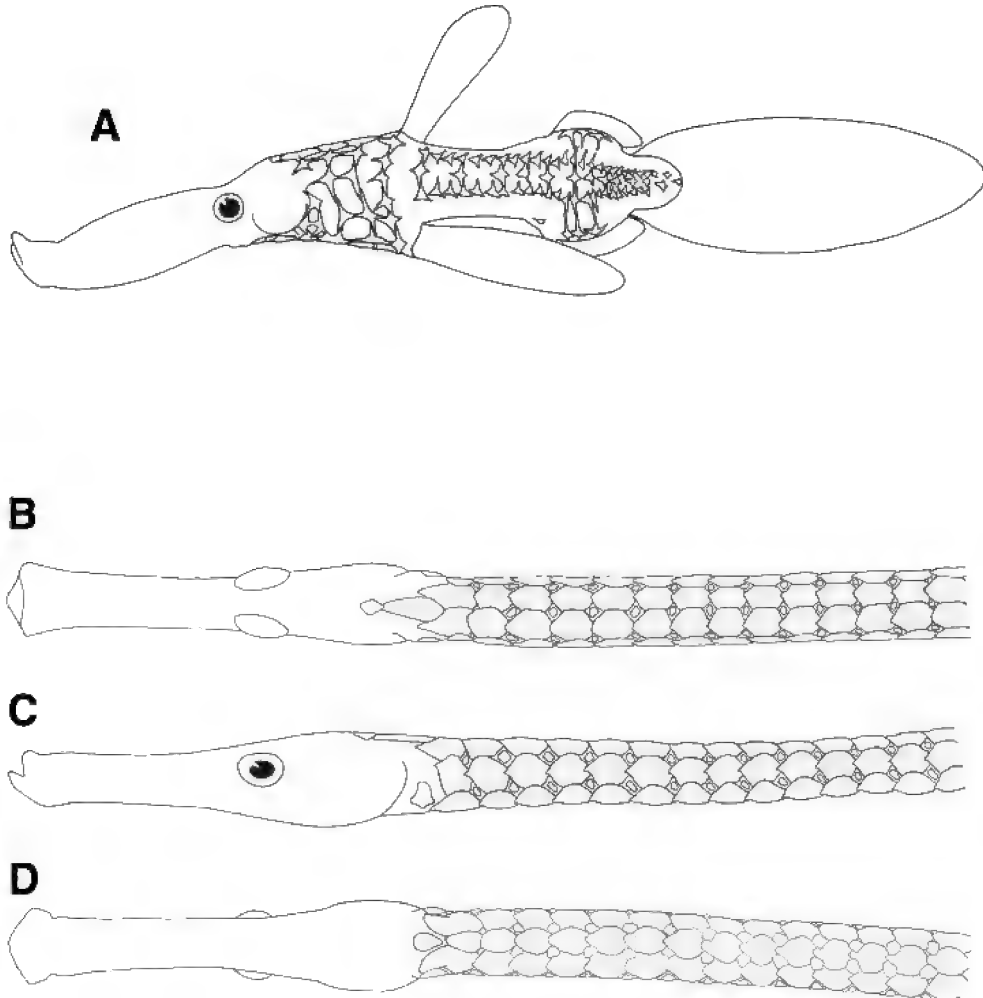
Fig. 16. Schematic representation of body armor of adult syngnathoids, continued. **A.** *Solenostomus cyanopterus*, lateral view, after Jungersen (1910). **B.** *Syngnathus typhle*, 121 mm (USNM 366873), dorsal view. **C.** Lateral view. **D.** Ventral view.

are paired pelvic plates. As with the dorsal series, most plates of the ventral series arise from expansions of the proximal-middle radials as follows, rostrocaudally: one plate from the pterygiophore supporting the single supernumerary anal spine, which also serially supports the first of seven anal soft rays, six plates from pterygiophores serially supporting the remaining six anal soft rays, nine from rayless pterygiophores, and the remaining eight plates from expanded hemal spines.

The body armor of *Gasterosteus* (fig. 17D) develops in a fashion similar to that of *Spinachia*. The plates of the dorsal series arise from expansions of the proximal-middle radials as follows, rostrocaudally: two anterior plates from rayless pterygiophores, two plates from the pterygiophores supporting the two large dorsal spines, a smaller plate from a rayless pterygiophore, a small plate from the pterygiophore supporting the third dorsal-fin spine, a large number of plates (12 in the specimen we figure) from the pterygiophores serially supporting the dorsal soft rays, and one plate from a rayless pterygiophore. The number of plates arising from the pterygiophores of the soft dorsal fin and succeeding rayless pterygiophores varies among
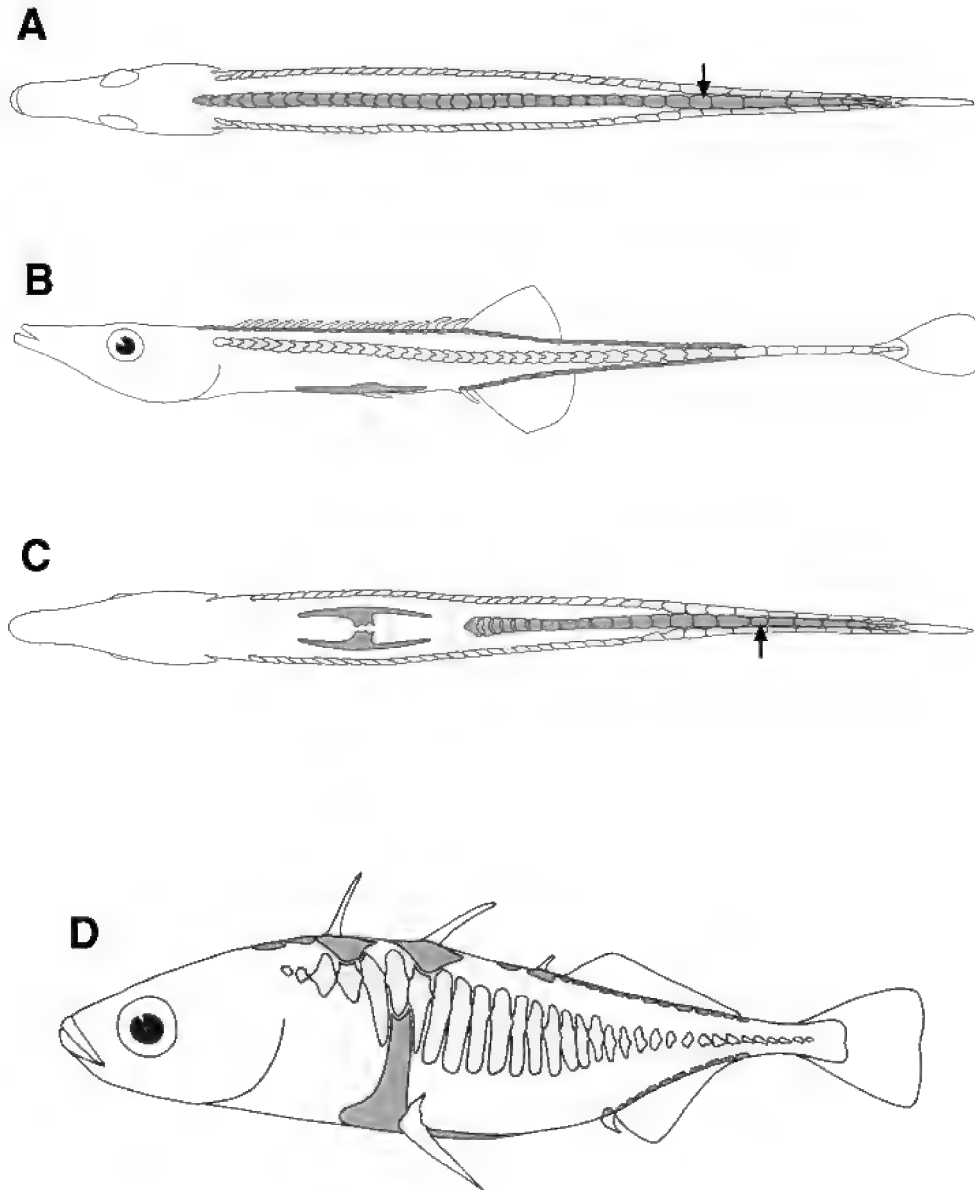
Fig. 17. Schematic representation of body armor of gasterosteids. **A.** *Spinachia spinachia*, 90 mm (USNM 366871), dorsal view. **B.** Lateral view. **C.** Ventral view. **D.** *Gasterosteus aculeatus*, 42 mm (ZMB 24126), lateral view. Exoskeletal components light gray, endoskeletal components darker gray, arrows point to first plates originating from neural or hemal spines.

taxa (and individuals) and is correlated with numbers of fin rays. The paired lateral series consists of a variable number of plates (32 in the specimen we figure). Large paired pelvic plates are developed. As with the dorsal series, the unpaired plates of the ventral series arise from expansions of the proximal-middle radials as follows, rostrocaudally: one anterior plate from the pterygiophore that supports the single supernumerary anal spine, which also serially supports the first anal soft ray, followed by a series of plates from the pterygiophores supporting the soft rays of the anal fin (nine in the specimen we
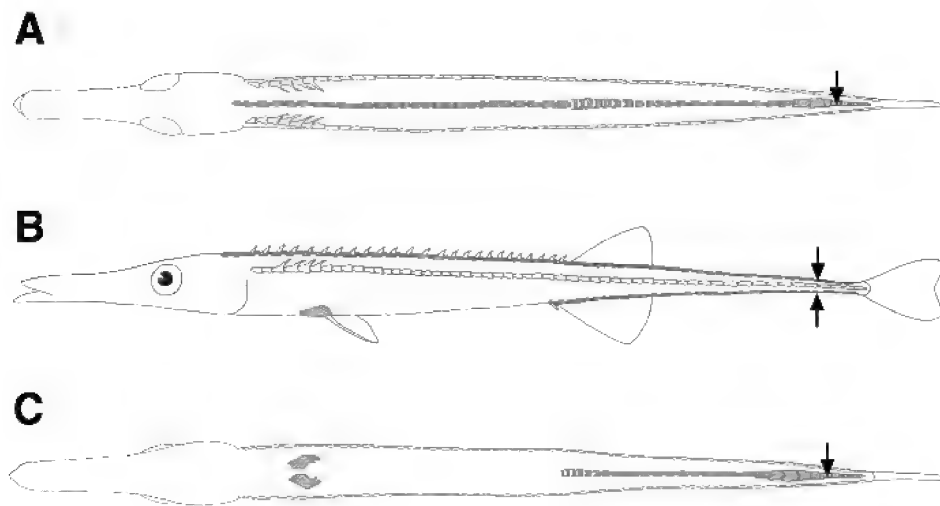
Fig. 18.   Schematic representation of body armor of aulorhynchids. **A.** *Aulorhynchus flavidus*, 92 mm (BMNH 1979.7.20.7), dorsal view. **B.** Lateral view. **C.** Ventral view. Exoskeletal components light gray, endoskeletal components darker gray, arrows point to first plates originating from neural or hemal spines.

figure) and one (in the specimen we figure) or more plates from succeeding rayless pterygiophores.

The body armor of aulorhynchids greatly resembles that of gasterosteids, especially that of *Spinachia*, a basal gasterosteid according to Bowne (1994). We illustrate *Aulorhynchus flavidus* (fig. 18). Its body armor consists of a dorsal unpaired row, lateral paired rows, an unpaired ventral row, and paired pelvic plates. The plates of the dorsal series arise from expansions of the proximal-middle portion of the pterygiophores or from expanded neural spines as follows, rostrocaudally: 2 anterior plates from rayless pterygiophores, 25 plates from the pterygiophores supporting the series of 25 dorsal spines supernumerarily, the last of which also serially supports the first of ten dorsal soft rays, 9 plates from the pterygiophores serially supporting the remaining nine dorsal soft rays, 14 plates from rayless pterygiophores, and 4 plates from expanded neural spines. The paired lateral series consists of 55 plates housing the lateral line canal. Comparatively small paired pelvic plates are developed. The unpaired plates of the ventral series arise from expansions of the proximal-middle portion of the pterygiophores and expanded hemal spines as follows, rostrocaudally: 1 an-

terior plate from the pterygiophore that supports the single supernumerary anal spine, which also serially supports the first of 10 anal soft rays, followed by a series of 9 plates from the pterygiophores supporting the remaining nine anal soft rays, 14 plates from succeeding rayless pterygiophores, and finally 4 plates from expanded hemal spines.

The body armor of *Indostomus* differs from that of syngnathoids in the following ways: (1) The dorsal and ventral unpaired series are formed by expanded proximal-middle radials of either rayless, spinous ray, or soft ray-bearing pterygiophores, or expanded neural and hemal spines and thus have an endoskeletal origin. The dorsal and ventral series in syngnathoids are either paired or unpaired but represent dermal plates in the skin that lack any connection to the endoskeleton. Exceptions may be the unpaired series in front of the dorsal fin in *Solenostomus* or the few so-called nuchal plates in pipefishes; however, their ontogeny is not known. (2) There is only one paired series of lateral plates of dermal origin in *Indostomus*, whereas there are usually two or more series of dermal lateral plates in syngnathoids. (3) *Indostomus* possesses large paired plates developing from the pelvic girdle, whereas syngnathoids lack these.

In contrast, the body armor of *Indostomus* shares several notable similarities with that of gasterosteoids: (1) All or most of the unpaired plates in the dorsal and ventral series form from expanded proximal-middle radials, either rayless or bearing supernumerary fin spines or serially associated soft rays. In some gasterosteoids (*Aulorhynchus*, *Aulichthys*, *Spinachia*, *Pungitius*) the last few plates in these series form from expanded neural and hemal spines. (2) When lateral plates are present, they are represented by a single series of lateral dermal ossifications. (3) Paired plates arise as membranous outgrowths of the pelvic girdle.

We conclude that the "remarkable similarity" of the body armor of *Indostomus* and the Syngnatha is superficial. Our study reveals that in both adult arrangement and development the body armor of *Indostomus* is most like that of gasterosteoids which, to our knowledge, is unique among acanthomorphs, particularly in the origin of the dorsal and ventral series, and the pelvic plates.

LOWER JAW DEPRESSION EXCLUSIVELY VIA THE HYOID

Pietsch (1978: 527) listed nine derived character states for his Syngnatha, in which he included the Pegasidae, Solenostomidae, and Syngnathidae. The first of these was described as "a feeding mechanism involving a single coupling by way of the hyoid apparatus, the interopercle being widely separated from the reduced subopercle." Johnson and Patterson (1993: 577–578) confirmed that character noting that in those groups "the interopercle is reduced to a thin rod, decoupled from the remaining opercular bones, and is attached to the hyoid exclusively by the interoperculohyoid ligament." Furthermore, for reasons discussed above, Johnson and Patterson regarded the bone identified in *Indostomus* as the interopercle by Banister (1970) to be the preopercle and the preopercle to be a circumorbital. They thus concluded that the decoupling characteristic of Syngnatha is shared by *Indostomus*, where it is effected through absence of the interopercle, suggesting that the two taxa are closely related. The above description of the development of the hyopalatine arch in *Indostomus*, however, shows clearly that Johnson and Patterson's (1993) circumorbital arises in the typical position of the preopercle, that is posterior to the hyopalatine arch far removed from the orbit. It only later expands anteriorly. Johnson and Patterson's (1993) preopercle ossifies in the ligament between the hyoid and the lower jaw and thus shows the typical arrangement of an interopercle.

In summary, *Indostomus* has a well-developed interopercle that is not decoupled from the remaining opercular bones. The bone hypothesized to be an infraorbital by Johnson and Patterson (1993) is the preopercle, as originally proposed. Therefore, the above character is not a valid synapomorphy for *Indostomus* and the Syngnatha.

LARGE NASAL BONES FUSED IN THE MIDLINE

In his description of the osteology, Pietsch (1978: 519) stated that "The elongate nasal bones of *Pegasus* are united to the frontal bones by dentate sutures and fused on the midline to form a beak or rostrum . . . ". He also noted that "The large median bone covering the dorsal surface of the snout of *Indostomus* (ethmoid of Banister, 1970) is most likely a pair of large nasal bones fused on the mid-line (as in the Pegasidae)," lending support to the possibility that the two are closely related. Banister (1970) regarded the nasals to be absent in *Indostomus* and considered the unpaired median bone to be the ethmoid (= mesethmoid) fused with the dermal supraethmoid (= dermethmoid, median rostral), but neither he nor Pietsch had ontogenetic information on pegasids or indostomids. Our description of the development of the skull in *Indostomus* clearly shows that the medial element in question arises as paired dermal ossifications in the snout region, as with typical nasals. During subsequent development these two bones first fuse along their midline, and eventually the anterior end of this complex ossification fuses with the vomer. We conclude that the large median bone in the snout region of *Indostomus* represents fused nasals as proposed by Pietsch, but the ontogeny of the bone claimed to be fused nasals in pegasids is unfortunately still unknown. We note, however,

that in *Indostomus* the bone we consider to represent fused nasals develops in a fashion very different from that of typical teleost nasals and it also lacks any evidence of a lateral-line canal. In contrast, the fused nasals in pegasids carry a lateral-line canal and remain separate from the vomer. Accordingly, we do not want to exclude the possibility that our "nasal" in *Indostomus* could actually represent the mesethmoid. This interpretation requires the assumption that the mesethmoid here bears two posterior processes of membrane bone that either ossify earlier than the body of the bone (fig. 2) or are better calcified and can thus be detected easier (and earlier) with the method of clearing and double-staining.

ONTOGENY OF SOME OTHER PERTINENT CHARACTERS

Johnson and Patterson (1993) noted three specialized features that are "unique to *Indostomus* and *Pegasus* among gasterosteiforms." We list them followed by our observations of their ontogeny in *Indostomus*, which provides no new insight about their homology. (1) Subopercle reduced to a thin splint of bone lying posteromedial to the opercle (figs. 4, 5). The subopercle of *Indostomus* is relatively long but very narrow in all ontogenetic stages we studied from the smallest larva (3 mm) to the largest juvenile (16.6 mm), extending from the upper to the lower tip of the posterior face of the opercle. It becomes relatively much shorter by the adult stage, where it is reduced to a small splint of bone confined to the posterodorsal corner of the opercle. (2) Relatively enlarged fourth epibranchial (fig. 6). The fourth epibranchial is enlarged relative to the other three epibranchials already at its earliest appearance in ontogeny (3 mm). (3) Presence of only three pectoral radials (fig. 8B, C). As described above, three radials ossify within the pectoral radial plate relatively late in development (not ossified at 11.2 mm, present at 16.6 mm).

Banister (1970: 192) did not mention a parietal in his description of the braincase of *Indostomus*, nor did he show one in his illustration (Banister, 1970: fig. 10) of its dorsal surface. His list of characters in which

Indostomus differs from *Aulorhynchus* (Banister, 1970: 198) makes it clear that he recognized that *Indostomus* lacks a separate parietal, and his list of trends shared with the "batrachoid lineage," (Banister, 1970: 201) indicates that he thought its absence to be the result of fusion with the epioccipital. In our ontogenetic series the epioccipitals first appear in a 6.4-mm specimen as circular perichondral ossifications, are large and well ossified by 11.2 mm, and a parietal is lacking at all stages. Thus, there is no evidence that a parietal develops and fuses with the epioccipital during ontogeny.

Indostomus is unusual among teleosts in that the hyopalatine arch comprises a single large, elongate bone anterior to the quadrate (fig. 5C). Banister (1970: 193) called this bone the "pterygoid," and noted that it "fills the places usually occupied by the ectopterygoid, endopterygoid and palatine." Because no separate centers of ossification were evident in his adult specimen, he concluded that "the real identity of the bone must remain hidden until young stages can be found." As described above, our ontogenetic series clearly demonstrates that this bone develops from a single center of ossification ventral to the pterygopalatine cartilage and therefore represents the ectopterygoid. An endopterygoid and palatine are lacking in *Indostomus*, and even the cartilaginous precursor of the autopalatine, the maxillary process of the pars autopalatina, never develops. We have no developmental information for most gasterosteoids (including *Hypoptychus*), but the endopterygoid is clearly lacking in adults of all genera and in our ontogenetic series of *Aulorhynchus* (4.2 mm NL–38.5 mm), *Gasterosteus* (5.6 mm NL–40 mm), and *Spinachia* (19–33 mm). Orr (1995: 610, fig. 163) reported and illustrated an endopterygoid in *Hypoptychus*, but our examination of several specimens indicates that he was mistaken. We did not examine Orr's material, but conjecture that the bone he illustrated and identified as the endopterygoid in *Hypoptychus* is part of a thin, horizontal, laminar expansion of the lateral ethmoid that extends well forward of the main body of that bone. If this lamina was inadvertently cut through and removed during dissection of the suspensorium, it would occupy a position similar to

that of the bone labeled endopterygoid by Orr, substantially farther forward in relation to other bones of the suspensorium than is typical for teleosts. He also reported that, uniquely among syngnathoids, aulostomids and pegasids lack an endopterygoid; we have confirmed this in adult representatives of those two families, but we have not checked its distribution among all syngnathoids.

Banister (1970) considered the elongate bony neural and hemal canals in *Indostomus* to be neural and hemal arches, respectively. We have shown above that these canals originate ontogenetically from two different sources: (1) neural and hemal arches that develop a median caudally directed horizontal extension at their tips (most likely the neural and hemal spines, respectively), and (2) long postzygapophyses that fuse with these extensions. We have no ontogenetic information on vertebral formation in other gasterosteiforms and thus cannot currently evaluate the phylogenetic significance of this finding.

CONCLUSIONS

Our ontogenetic study of the skeleton of *Indostomus* has resolved several important questions of homology. A number of putative synapomorphies for different hierachical levels in the gasterosteiforms were demonstrated to be invalid. There is currently no doubt that *Indostomus* is a member of the Gasterosteiformes, and we have presented evidence that points to gasterosteoid affinities. Perhaps the most compelling is the remarkable similarity between *Indostomus* and gasterosteoids in the structure and development of the body armor, a character complex that is unique among fishes. Fusion of the pectoral radial plate to the scapulocoracoid and ossification of the pectoral radials without prior fragmentation of the larval fin cartilage represent another complex specialization uniquely shared by the two taxa.

On the basis of current evidence, then, we strongly favor the hypothesis that *Indostomus* is a gasterosteoid. We found no apomorphies that *Indostomus* shares uniquely with the Syngnathoidei, and we think that the three pectoral radials, the reduced subopercle, the enlarged fourth epibranchial, and putative fused nasals shared with pegasids and

the basal fusion of gill filament blades shared with Syngnatha (see Johnson and Patterson, 1993: 574–577) are homoplasies. The precise placement of *Indostomus* within the Gasterosteoidei awaits future investigations. While working through the literature and examining our material, we have encountered numerous homology problems in the gasterosteiform skeleton that have significantly influenced ideas about relationships of the component subgroups. We are convinced that a reasonable hypothesis of gasterosteiform intra- and interrelationships can only be reached once these problems are scrutinized in a way similar to what we have done here for *Indostomus*, requiring detailed ontogenetic studies of the skeleton of all representatives.

ACKNOWLEDGMENTS

REFERENCES

Banister, K.E. 1970. The anatomy and taxonomy of *Indostomus paradoxus*. Bulletin of the British Museum of Natural History 19: 179–209.

Berg, L.S. 1958. System der rezenten und fossilen Fischartigen und Fische. Berlin: VEB Verlag, 310 pp.

Bertin, L., and C. Arambourg. 1958. Super-ordre des téléostéens. *In* P.-P. Grassé (editor), Traité de zoologie, 13, part 3: 2204–2500. Paris: Masson et Cie.

Bolin, R.L. 1936. The systematic position of *Indostomus paradoxus* Prashad and Mukerji, a fresh water fish from Burma. Journal of the Washington Acadademy of Sciences 26: 420–423.

Bowne, P.S. 1994. Systematics and morphology of the Gasterosteiformes. *In* M.A. Bell and S.A. Foster (editors), The evolutionary biology of the threespine stickleback: 28–60. New York: Oxford University Press.

Britz, R. 2000. Aspects of the reproduction and development of *Indostomus paradoxus* (Teleostei: Indostomidae). Ichthyological Explorations of Freshwaters 11: 305–314.

Britz, R., and M. Kottelat. 1999. Two new species of gasterosteiform fishes of the genus *Indostomus* (Teleostei: Indostomidae). Ichthyological Explorations of Freshwaters 10: 327–336.

de Beer, G.R. 1937. The development of the vertebrate skull. Oxford: Oxford University Press. Paperback reprint. Chicago: University of Chicago Press, 1985, xlvi + 554 pp. + 143 pls.

Fraser, T.H. 1972. Some thoughts about the teleostean fish concept—the Paracanthopterygii. Japanese Journal of Ichthyology 19: 232–242.

Fritzsche, R.A. 1976. A review of the cornetfishes, genus *Fistularia* (Fistulariidae), with a discussion of intrageneric relationships and zoogeography. Bulletin of Marine Science 26: 196–204.

Fujita, K. 1990. The caudal skeleton of teleost fishes. Tokyo: Tokai University Press, xiii + 897 pp.

Gaupp, E. 1906. Die Entwickelung des Kopfskelettes. *In* O. Hertwig (editor), Handbuch der vergleichenden und experimentellen Entwickelungslehre der Wirbeltiere, 3. Band, 2. Teil, 7. Kapitel: 573–890. Jena: Gustav Fischer.

Grandel, H., and S. Schulte-Merker. 1998. The development of the paired fins in the zebrafish (*Danio rerio*). Mechanisms of Development 79: 99–120.

Greenwood, P.H., D.E. Rosen, S.H. Weitzman, and G.S. Myers. 1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. Bulletin of the American Museum of Natural History 131: 339–456.

Johnson, G.D., and E.B. Brothers. 1993. *Schindleria*: a paedomorphic goby (Teleostei: Gobioidei). Bulletin of Marine Science 52: 441–471.

Johnson, G.D., and C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bulletin of Marine Science 52: 554–626.

Jungersen, H.F.E. 1908. Ichthyotomical contributions. I. The structure of the genera *Amphisile* and *Centriscus*. Det Kongelige Danske Videnskabernes Selskabs Skrifter, 7. Raekke, Naturvidenskabelig og Matematisk Afdeling VI 2: 41–109.

Jungersen, H.F.E. 1910. Ichthyotomical contributions. II. The structure of the Aulostomidae, Syngnathidae and Solenostomidae. Det Kongelige Danske Videnskabernes Selskabs Skrifter, 7. Raekke, Naturvidenskabelig og Matematisk Afdeling VIII 5: 269–363.

Leviton, A.E., R.H. Gibbs, E. Heal, and C.E. Dawson. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985: 802–832.

McClelland, J. 1839. Indian Cyprinidae. Asiatic Researches 19: 217–471.

Nelson, J.S. 1971. Comparison of the pectoral and pelvic skeletons and of some other bones and their phylogenetic implications in the Aulorhynchidae and Gasterosteidae (Pisces). Journal of the Fisheries Research Board of Canada 28: 427–442.

Orr, J.W. 1995. Phylogenetic relationships of gasterosteiform fishes (Teleostei: Acanthomorpha). Unpublished Ph.D. dissertation, University of Washington, Seattle, 813 pp.

Patterson, C. 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. Philosophical Transactions of the Royal Society of London Series B Biological Sciences 269: 275–579.

Patterson, C. 1977. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton. Linnean Society Symposium Series 4: 77–121.

Pietsch, T.W. 1978. Evolutionary relationships of the sea moths (Teleostei: Pegasidae) with a classification of gasterosteiform families. Copeia 1978: 517–529.

Potthoff, T., and J.A. Tellock. 1993. Osteological development of the snook, *Centropomus undecimalis* (Teleostei, Centropomidae). Bulletin of Marine Science 52: 669–716.

Potthoff, T., S. Kelley, M. Moe, and F. Young. 1984. Description of porkfish larvae (*Anisotremus virginicus*, Haemulidae) and their osteo-

logical development. Bulletin of Marine Science 34: 21–59.

Potthoff, T., S. Kelley, V. Saksena, M. Moe, and F. Young. 1987. Description of larval and juvenile yellowtail damselfish, *Microspathodon chrysurus*, Pomacentridae, and their osteological development. Bulletin of Marine Science 40: 330–375.

Potthoff, T., S. Kelley, and L.A. Collins. 1988. Osteological development of the red snapper, *Lutjanus campechanus* (Lutjanidae). Bulletin of Marine Science 43: 1–40.

Prashad, B., and D.D. Mukerji. 1929. The fish of the Indawgyi Lake and the streams of the Myitkyina District (Upper Burma). Records of the Indian Museum Calcutta 31: 216–219.

Rendahl, H. 1930. Pegasiden-Studien. Arkiv för Zoologi 21A: 1–56.

Roberts, C.D. 1993. Comparative morphology of spined scales and their phylogenetic significance in the Teleostei. Bulletin of Marine Science 52: 60–113.

Springer, V.G., and G.D. Johnson. 2000. Use and advantages of ethanol solution of alizarin red S dye for staining bone in fishes. Copeia 2000: 300–301.

Taylor, W.R., and G.C. Van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9: 107–119.

$\rightarrow$

Plate 1. *Indostomus paradoxus*, C&S specimens (USNM 366869). **A.** Snout region of 4.8-mm specimen, dorsal view, separate ossification centers of nasals. **B.** Snout region of 5.5-mm specimen, dorsal view, arrow marks zone of fusion between nasal bones. **C.** Snout region of 5.3-mm specimen, dorsal view, nasals fused with each other and with vomer. **D.** Same specimen, dorsal view, articulation between occiput and first vertebra, arrows point to posteriorly projecting pointed processes of membrane bone of exoccipitals. **E.** Head region of 4.3-mm specimen, lateral view, arrows mark subopercle. **F.** Same specimen, close-up of interopercular region. **G.** Head region of 6.8-mm specimen, lateral view, arrows mark subopercle. **H.** Same specimen, close-up of interopercular region, arrow points to mandibulohyoid ligament between interopercle and lower jaw.
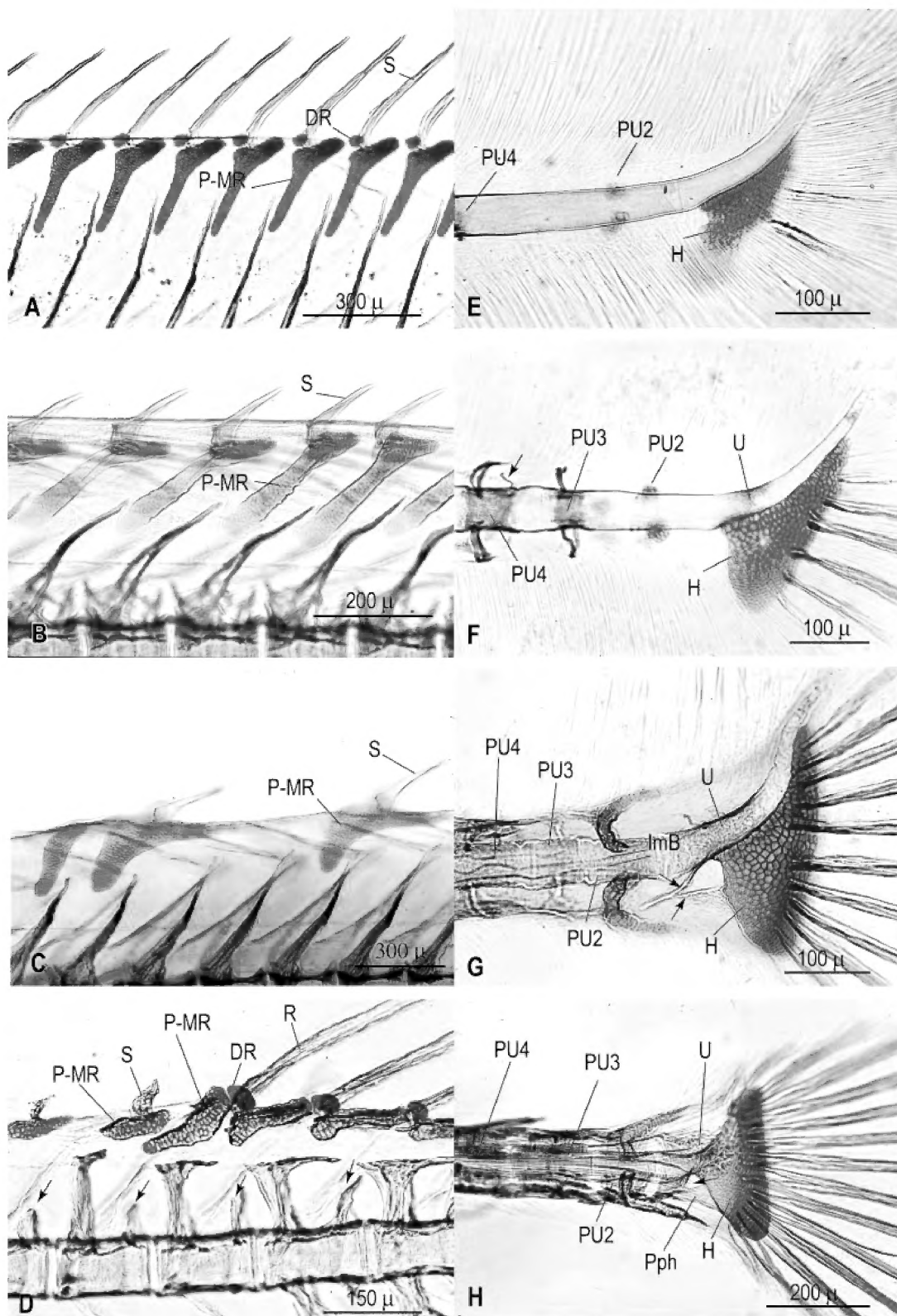
→
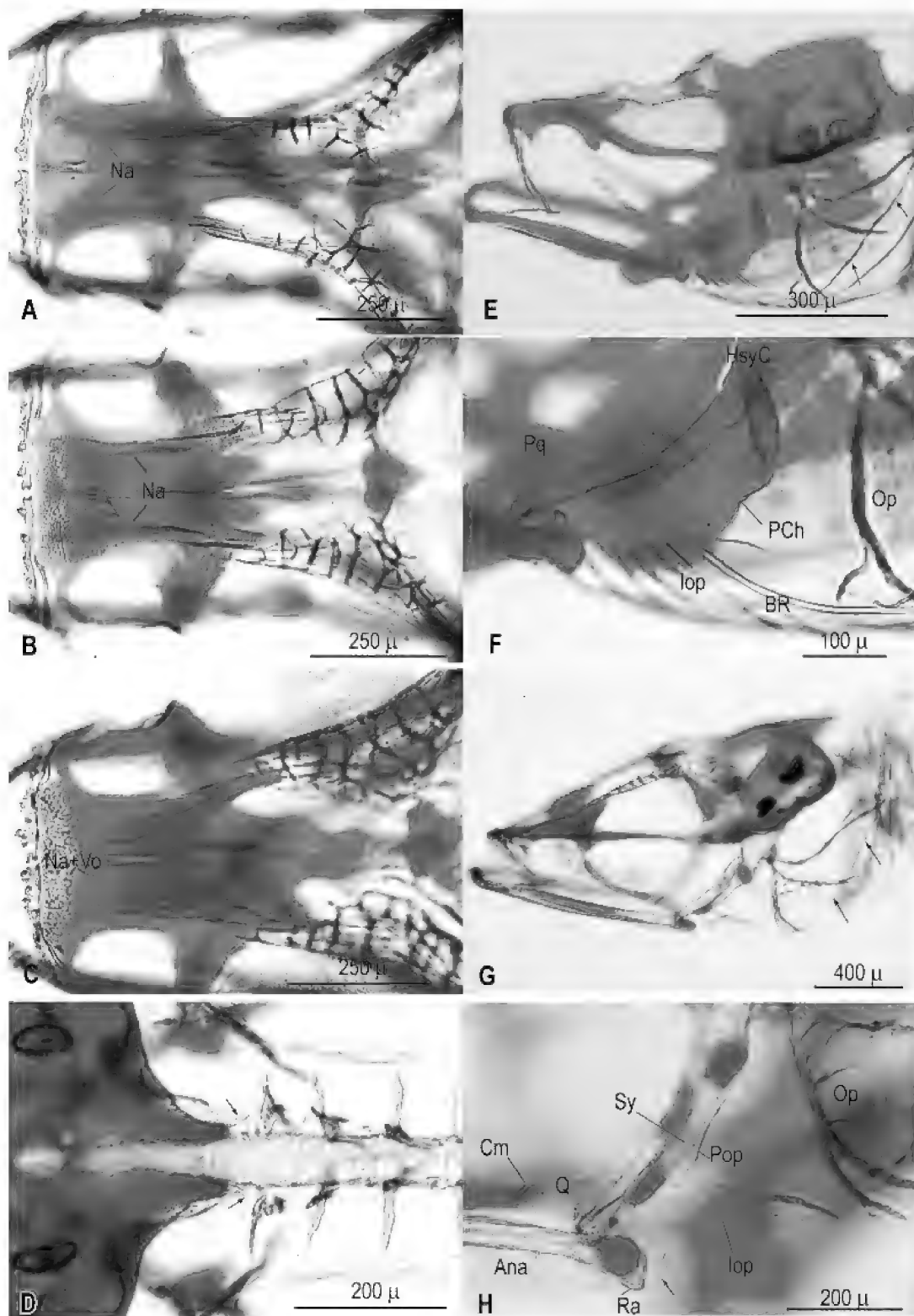
Plate 2.   *Indostomus paradoxus*, C&S specimens (USNM 366869). **A.** Junction of abdominal-caudal region of 3.5-mm specimen, lateral view, note anteroposteriorly flattened and expanded neural and hemal spines in caudal region. **B.** Abdominal region of 5.3-mm specimen, lateral view, five lateral plates present in the lateral body wall, dorsal and ventral plates of the caudal region with spinules. **C.** Same specimen, close-up of five lateral plates, lateral view. **D.** Same specimen, anterior pterygiophores of soft dorsal fin, dorsal view, arrows mark lateral expansion of membrane bone of proximal-middle radials. **E.** 5.5-mm specimen, dorsal view, expanded neural spines of PU4—PU6 with lateral spinules, PU3 and PU7 partly visible. **F.** Abdominal region with five lateral plates of 6.8-mm specimen, ventral view; note anal plate in wall of body cavity anterior to first anal pterygiophore. **G.** Abdominal region of 8.7-mm specimen, lateral view, cleithrum expanded and its surface ornamented, seven lateral body plates present, pelvic plate has formed. **H.** Close-up of right side pelvic cartilage with membranous ornamented outgrowth of pelvic plate.

$\rightarrow$
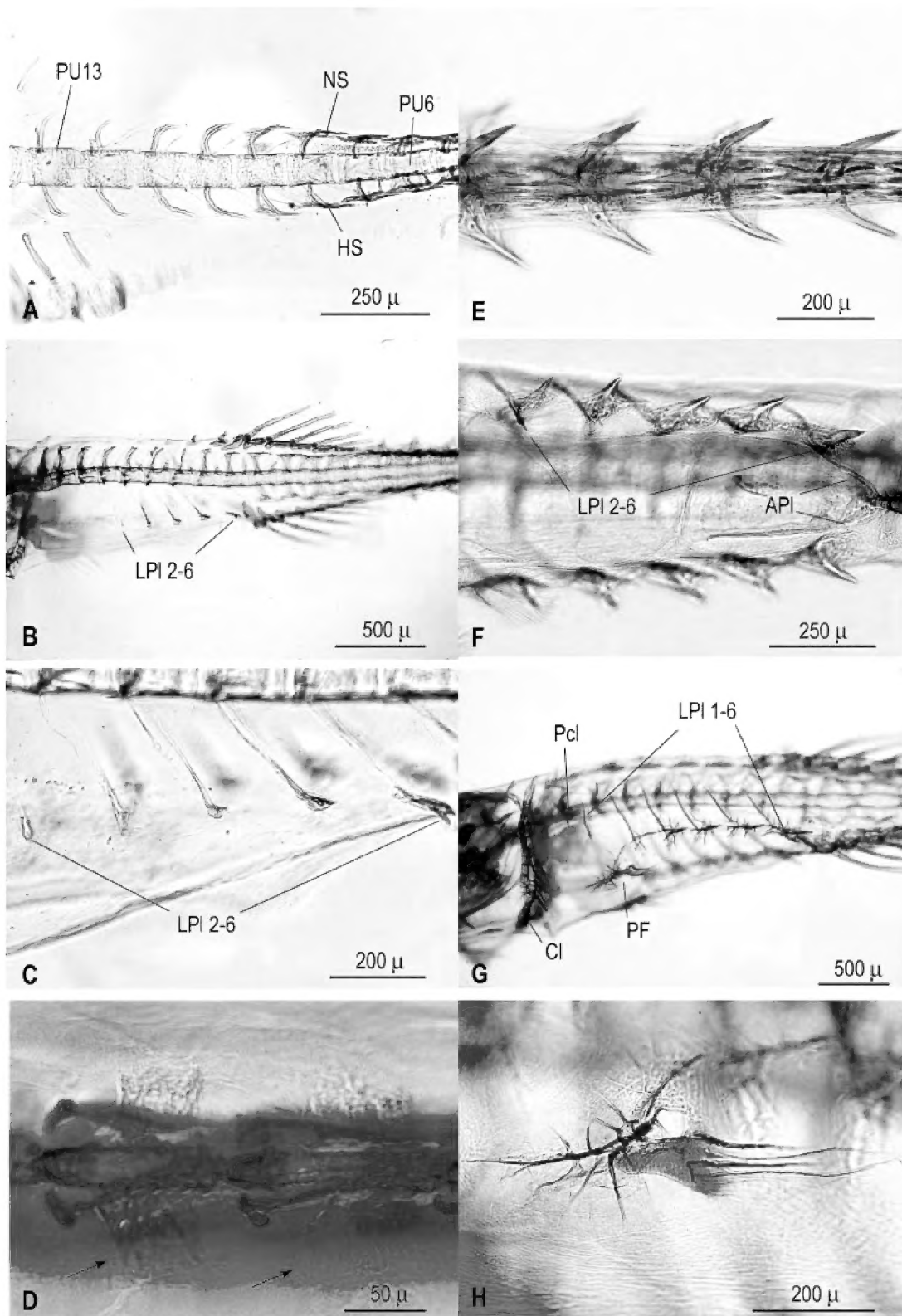
Plate 3.   **A–D.** Ontogenetic stages of dorsal-fin spine articulation in selected percomorph and smegmamorph taxa, C&S specimens, lateral view. **A.** *Ctenopoma* cf. *pellegrini* (family Anabantidae), 8 mm (USNM 367057). **B.** *Macrognathus pancalus* (family Mastacembelidae), 16.7 mm (USNM 367058). **C.** *Gasterosteus aculeatus*, 10.3 mm (USNM 366872). **D.** *Indostomus paradoxus*, 5.3 mm (USNM 366869), arrows point to dorsal postzygapophyses. **E–H.** *Indostomus paradoxus*, ontogeny of caudal fin, C&S specimens (USNM 366869). **E.** 3.3 mm. **F.** 3.8 mm, arrow at PU4 points to developing dorsal postzygapophysis. **G.** 4.3 mm, arrows point to membranous outgrowths of centrum and hypural. **H.** 5.5 mm, arrow marks foramen of pseudoparhypural for passage of caudal artery.